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Effects of climate-related stressors and pollutants on social behaviour in gregarious fishes

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MSci

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Abstract

Anthropogenic activities have far-reaching impacts on natural systems and have documented effects on physiology and behaviour for aquatic animals. In fish species, gregarious behaviour in the form of shoaling or schooling is a key adaptive trait, with benefits including foraging and predator evasion. As anthropogenic impacts become increasingly ubiquitous, the effects of these stressors on adaptive traits such as social behaviour are of urgent research interest. Climate-related stressors, linked directly or indirectly to anthropogenic climate change, include high temperatures, hypoxia, and acidification. These may affect shoaling behaviour through effects on metabolic rate or neurological functioning. Alongside climate-related stressors, the incidence of anthropogenic pollutants in aquatic systems has increased markedly in recent years. Chemical pollutants include organic or inorganic substances and mixtures of these, which may have metabolic, endocrine, or neurological effects. Non-chemical pollutants such as light, noise, and turbidity can cause stress-related changes in behaviour, and interfere with detection of conspecifics and thus shoaling efficiency. As the occurrence of individual stressors becomes more frequent, stressor combinations are also increasingly observed and the potential effects of these on ecosystems are of emerging research interest. For gregarious species, the social context is an essential consideration for determining the ecological effects of anthropogenic stressors. While the primary physiological and behavioural impacts of stressors act at the level of the individual, their effects on ecological interactions often manifest at the level of the group. Understanding how stressor effects on individuals translate to impacts on shoaling dynamics is therefore essential to predicting ecological impacts in gregarious species. Consolidating the current level of knowledge in this field is a key first step in determining research gaps and opportunities for further study. In addition, despite the importance of social context, effects of anthropogenic stressors on fish social behaviour at the individual and group levels have rarely been empirically linked. The degree of prior research is also highly variable among stressors, with further study urgently needed on artificial light at night (ALAN) and stressor combinations.

In this thesis, I aimed to identify gaps in the literature surrounding the effects of anthropogenic stressors on fish social behaviour by first conducting systematic reviews of published studies. I then use lab-based observations to address the need for studies linking individual- and group-level behaviours in gregarious fish in the context of two climate-related stressors, temperature and hypoxia. Finally, I examine the effects of an

understudied stressor, ALAN, on sociability and risk-taking behaviour in a gregarious reef fish.

In chapter 1, I introduce the impacts of different anthropogenic stressors on fish species. I also describe the relevance of social behaviour, and the importance of social context in gregarious species. I highlight key knowledge gaps, and challenges associated with studying the effects of anthropogenic stressors on social behaviour.

Chapter 2 consists of a meta-analysis conducted on studies of the effects of climate-related stressors on fish social behaviour. A systematic search revealed 45 studies of temperature, acidification, and/or hypoxia. My findings show that group cohesion is negatively correlated with oxygen concentration in fish species but did not reveal effects of temperature or acidification on social behaviour. Temperature was better-studied than other stressors, and studies of multiple stressors were few.

In chapter 3, I expand my review of the literature to studies of the effects of anthropogenic pollutants on fish social behaviour. A total of 165 studies were identified, with a large number of studies of organic pollutants ($n = 92$). Both organic and inorganic pollutants were associated with reduced sociability, while exposure to mixed pollutants led to increased sociability but reduced group cohesion. Among non-chemical pollutants, no effect of turbidity was found, but sociability decreased with light exposure. The effect of noise pollution was dependent on duration, as group cohesion decreased with longer exposure time.

In chapter 4, I sought to address a knowledge gap identified in chapter 2 by linking changes in individual behaviour across conditions of temperature with behaviour of those same individuals in a shoal. Using a model species, rummy-nose tetra *Hemigrammus rhodostomus*, I carried out assays of sociability and risk-taking behaviour at three temperatures (24°C, 27°C, and 30°C) for each individual. Groups comprised of the same individuals used in sociability and risk-taking behaviour assays were then observed at the same three temperatures for shoaling behaviour. Both individuals and groups became more active at higher temperatures. Response to temperature in groups was also influenced by behaviour displayed in individual trials, however, with social, less-active fish becoming less active at high temperatures.

In chapter 5, I carried out a similar experiment to that described in chapter 4, to investigate the effects of hypoxia on links between individual and group behaviour in *H. rhodostomus*. Fish were assayed alone and in groups at three levels of oxygen saturation (100%, 70%, and 30%). Under hypoxia, fish generally became less active and inter-individual distances in shoals decreased. Individuals that displayed high risk-taking behaviour were more active in group behaviour trials under hypoxia, however, indicating that individual behavioural traits may modulate shoaling responses to abiotic stressors.

Based on the low number of studies of ALAN found in my review of the literature, chapter 6 describes an experiment investigating the effects of chronic exposure to ALAN in the wild on a gregarious reef fish, *Dascyllus trimaculatus*. Fish were subjected to a sociability test, and an emergence test from a shelter following a chase stimulus. No effect on sociability was found, but ALAN-exposed fish were faster to emerge from a shelter following a chase stimulus. This increase in risk-taking behaviour may indicate a response to greater metabolic needs, high stress levels, or selective mortality in ALAN-exposed fish.

In chapter 7, I review my key results and summarise the role of this thesis in advancing the study of fish social behaviour. I then discuss the implications of my findings and contextualise the results of my experimental chapters with the trends identified from reviewing the literature. Finally, I reflect on the limitations of my thesis and the opportunities for future work.

As a whole, my thesis provides a summary of work conducted to date and begins to explore new avenues and fill knowledge gaps in the study of anthropogenic impacts on fish social behaviour. Using a combination of literature-based and experimental methods, my work shows general trends in stressor effects and highlights the importance of social context and intra- and interindividual variation in determining outcomes. Overall, this thesis both consolidates existing understanding of anthropogenic effects on a key adaptive behaviour in fishes and paves the way for future work addressing gaps in this understanding.

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Additional publications not included in this thesis

- Tiddy, I. C.**, Vidal, M., Mills, S. C., Beldade, R., Killen, S. S. (2026) Effects of artificial light at night on metabolic responses of a coral reef fish to a virtual predator. *Conservation Physiology* 14(1), coag045. <https://doi.org/10.1093/conphys/coag045>
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Declaration of Authorship

I declare that this thesis is the result of my own work, except where explicit reference is made to the work of others. This thesis has not been presented in any previous application for a degree at this or any other institution.

Signature:

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Co-authorship Statement

Chapter 2 author contributions: Izzy Tiddy conceived and designed the study, with assistance from Shaun Killen. Izzy Tiddy curated the dataset, with assistance from Daphne Cortese and Amelia Munson. Data collection, analysis, and visualisation were carried out by Izzy Tiddy. Izzy Tiddy wrote the original draft, with assistance from Michael Webster. All authors were involved in reviewing and editing subsequent drafts of the paper. A version of this paper is published in *Biological Reviews*: Tiddy, I.C., Munson, A., Cortese, D., Webster, M.M. and Killen, S.S. (2024), Impacts of climate-related stressors on social group cohesion and individual sociability in fish. *Biol Rev*, 99: 2035-2059.

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List of Abbreviations

ACS – Approaches to a conspecific shoal

ALAN – Artificial light at night

Cd – Cohen’s *d*

CEI – Clark-Evans Index

cm s⁻¹ – centimetres per second

DCS – Distance to conspecific shoal

DtCS – Distance travelled near a conspecific shoal

Hg – Hedge’s *g*

ID – Identity

IID – Inter-individual distance

LCS – Latency to approach a conspecific shoal

MDCS – Mean distance to the centre of the shoal

MD(N)S – Mean distance to (nearest) shelter

NND – Nearest neighbour distance

NTU – Nephelometric turbidity units

PC – Principal component

PCA – Principal component analysis

PSD – Pooled standard deviation

SD – Standard deviation

SL – Standard length

TA – Turning angle

TCS – Time near conspecific shoal

Chapter 1

General Introduction

1.1. Impacts of anthropogenic stressors in the aquatic environment

1.1.1. *Impacts of climate-related stressors in the aquatic environment*

As human influence becomes a near-inescapable part of the global landscape, we are becoming increasingly aware of the impacts of our activity on ecosystems. Globally, temperature anomalies have recently surpassed one year at or above the 1.5°C threshold set out in the Paris climate agreement for the first time (Cannon, 2025), with some projections indicating that long-term average temperatures may have already crossed this threshold (Bevacqua et al., 2025; Cannon, 2025). The impacts of a 1.5°C rise are already becoming apparent in many natural systems, threatening ecosystem diversity (Halsch et al., 2021; Warren et al., 2018), species richness (Price et al., 2024), and services upon which many human populations rely (Shivanna, 2020, 2022).

The focus of many climate studies is on highlighting lethal impacts of thermal stress, such as coral reef loss (Hughes et al., 2018; Obura et al., 2021) and shifts in primary and secondary production leading to food web collapse (Nagelkerken & Connell, 2015). Increasing concern is being raised, however, about the sublethal impacts of rising temperatures on ecosystems, particularly aquatic ecosystems (Alfonso et al., 2021). For ectothermic aquatic organisms, rising temperatures lead to higher metabolic costs, the impacts of which may be exacerbated by changes in food availability associated with climate change (Nagelkerken & Connell, 2015). While terrestrial temperature anomalies continue to alarm scientists (Bevacqua et al., 2025; Cannon, 2025), water bodies have historically provided a significant buffer to global heating by absorbing both carbon dioxide and heat (Gattuso et al., 2015; Shivanna, 2022; von Schuckmann et al., 2020).

An estimated 89% of global heat gain from 1971-2018 has occurred in the oceans (von Schuckmann et al., 2020), while increasing partial pressure of carbon dioxide in the atmosphere leads to greater concentrations of carbonate ions in water bodies, reducing water pH (Gattuso et al., 2015). While freshwater species are often better adapted to fluctuations in pH (Ishimatsu et al., 2004; Kwong et al., 2014), the impact of acidification on marine systems is expected to increase in coming years, with ocean pH projected to drop by 0.33 pH units by 2100 under a business-as-usual emissions scenario (Gattuso et al., 2015). For calcareous and siliceous organisms, this decrease in pH interferes with the

ability to construct bodily structures (Nagelkerken & Connell, 2015), and aquatic vertebrates such as fish have been found to experience interference with the functioning of sensory and cognitive systems related to ion imbalances (Jutfelt et al., 2013; Maulvault et al., 2018; A. Mitchell et al., 2022).

Alongside the threat of CO₂ itself, rising temperatures also go hand-in-hand with reduced oxygen availability (Gattuso et al., 2015), as the solubility of oxygen in water reduces at high temperatures. High temperatures can also lead to increased algal growth, leading to stripping of oxygen from an aquatic environment both by algal respiration and by aerobic bacteria as they consume plant matter following algal blooms (Levin et al., 2015).

Hypoxia, meaning low oxygen availability, or anoxia, meaning the complete lack of oxygen can have dramatic impacts on aquatic environments such as mass die-offs (Baladia et al., 2025; Godinho et al., 2019; McInnes & Quigg, 2010). More subtle, sub-lethal impacts also pose a threat to aquatic organisms, however, and aquatic respirators may struggle to meet their aerobic oxygen requirements during hypoxic periods (Domenici et al., 2017), leading to changes in behaviour to escape from or cope with stress (Domenici et al., 2002, 2017; Pineda et al., 2020). While hypoxia may be associated with temperature rise in aquatic systems, it is often exacerbated, particularly in freshwater and estuarine systems, by eutrophication (Levin et al., 2015). Eutrophication refers to the excessive input of nutrients, often from anthropogenic pollutants, to waterways, leading to algal blooms that remove oxygen from waterways as described above (Levin et al., 2015). Climate-related changes are therefore strongly linked to other anthropogenic stressors, with many aquatic ecosystems experiencing stressor combinations, the effects of which are not fully understood.

1.1.2. Impacts of pollutants in the aquatic environment

The issue of anthropogenic pollution, particularly in the form of chemical pollutants, has been highlighted in recent years by the increasing awareness of the ubiquity and risks of microplastics (Kye et al., 2023; W. Wang et al., 2019; Zhang et al., 2023), one form of chemical pollutant. The term “chemical pollutants”, however, refers to an enormous range of substances (Z. Wang et al., 2020; Zhang et al., 2023) that can enter aquatic systems through a number of avenues and sources (Zhang et al., 2023). Chemical pollutants can be very broadly grouped into organic and inorganic pollutants (Z. Wang et al., 2020). The former refers to carbon-based substances whose toxicity depends on their ability to be biotransformed by organisms following exposure (e.g., plastics, medicines, non-metallic

fertilisers) (Escher et al., 2011). Inorganic pollutants refer to metals and metal salts, which cannot be biotransformed, and are often introduced into aquatic systems as byproducts of industrial activity or agriculture (Shahjahan et al., 2022). Both can have lethal impacts on aquatic organisms, alongside a range of sublethal effects at lower concentrations (Bertram, Martin, et al., 2022a). These include impacts on fertility (Kidd et al., 2007), behaviour (Bertram, Martin, et al., 2022a; Firth et al., 2024), and cognitive functioning (Colovic et al., 2013; Valenti et al., 2012), alongside various metabolic effects depending on the substance and concentration (Escher et al., 2011; Orr et al., 2024; Shahjahan et al., 2022).

Chemical contamination may also interact with another abiotic factor in aquatic environments, turbidity, which refers to the level of suspended matter and thus degree of water clarity in an aquatic environment (Michael et al., 2021). Turbidity can cause reduced visibility, thus interfering with detection and response to movements of conspecifics (Chamberlain & Ioannou, 2019) or predators. In addition, increased suspended material may cause structural damage to gills (Cumming & Herbert, 2016; Hess et al., 2015) leading to reduced oxygen uptake. Some species have been found to plastically remodel gills to protect against suspended particles (Becke et al., 2018; Firth et al., 2024); however, this may interfere with regulation of ion exchange. Changes to oxygen uptake and ion balance may lead to altered neurosensory functioning, with associated impacts on shoaling responses (Jutfelt et al., 2013; Lucon-Xiccato et al., 2014; A. Mitchell et al., 2022).

In addition to chemical pollutants and turbidity, non-chemical pollutants such as anthropogenic light and noise may also have significant lethal and sublethal effects on aquatic life (Mickle & Higgs, 2018). Noise pollution is often recognised for its impact on cetaceans (Bittencourt et al., 2023; Holt et al., 2015; Papale et al., 2015), however other aquatic organisms also experience stress-related physiological (Wysocki et al., 2006), behavioural (Mickle & Higgs, 2018), and ecological impacts (Simpson et al., 2016). A 2009 study found low-frequency ambient ocean noise to be dominated by shipping sounds (Hildebrand, 2009), while human perception of global light pollution has increased by an estimated 7-10% per year from 2011 to 2022 (Kyba et al., 2023). In particular, the prevalence of light pollution in non-urban areas has grown significantly, leading to impacts on more remote terrestrial and aquatic systems (Davies et al., 2014; Marangoni et al., 2022). Light pollution may have direct behavioural impacts on aquatic organisms, such as attracting individuals and thus increasing transit time, as in hatchling turtles (Thums et al., 2016). Organisms such as insects may also congregate around lights, leading to changes in

foraging patterns of their predators (Buddendorf et al., 2026). Artificial light at night, or ALAN, disrupts sleep cycles and may lead to overactivation of the primary stress response (Kurvers et al., 2018), associating this form of pollution with a host of impacts such as changes in growth, metabolic rate, swimming capacity, and escape responsiveness (Georgiou et al., 2024; Kurvers et al., 2018; Schittko et al., 2026; Schligler et al., 2021; Schligler, Norin, et al., 2026; Schligler, Roost, et al., 2026).

Although the physiological impacts of anthropogenic pollutants on aquatic organisms are well-established, a vital component of the ecological effect of stressors is the translation of physiological changes into changes in behaviour. While physiological adaptation or acclimation may play a role in allowing organisms and therefore systems to compensate for the effects of stressors, behavioural responses to these stressors represent a key coping strategy for organisms such as fish (Bertram, Martin, et al., 2022b; Domenici et al., 2017).

1.2. Social behaviour in gregarious fish

1.2.1. Social group cohesion

While the range of behaviours displayed by fish are as diverse as the animals themselves, a common strategy for many fish species is social behaviour in the form of shoaling or schooling (Pitcher, 1983). Shoaling is defined as a loosely associated group of individuals, while schooling refers to a polarised group of fish displaying coordinated movements (Pitcher, 1983, 1986). Both behaviours are driven by an innate tendency to be “social”, i.e., to associate with other individuals, however (Pitcher, 1983, 1986). This distinguishes shoaling and schooling from aggregation, which refers to groups gathered around a specific resource or activity, such as breeding or foraging, rather than spontaneously formed as an expression of sociability (Pitcher, 1983). In group settings, the tendency of fish to shoal or school is often measured in terms of the distance among individuals, termed group cohesion, or the extent to which individuals face and swim in the same direction, termed group polarisation (Bartolini et al., 2015; Cook et al., 2014). Both metrics are linked to the speed of movement of the group, with faster-swimming groups generally displaying greater polarisation [Click or tap here to enter text.](#) (Kent & Ojanguren, 2015) but lower cohesion (Armstrong et al., 2019; Bartolini et al., 2015; Davis et al., 2019). Group cohesion may also depend on various factors, including the size of fish within groups (Romenskyy et al., 2017), the number of individuals in the group (Fu, 2016), and kinematic factors such as flow speed (Cao et al., 2025), as well as the behaviour of individuals within the group (Jolles, Weimar, et al., 2020).

1.2.2. *Individual behavioural traits relating to sociability*

Among gregarious fish species, group dynamics depend strongly on the behaviour of individuals within the group (Jolles et al., 2017), and the behaviours displayed by these individuals vary significantly at both the inter- and intra-individual levels (Jolles, Weimar, et al., 2020; Tiddy et al., 2025). Metrics of individual behaviour independently of conspecifics are therefore often used to assay traits of individuals that may inform their ecological interactions, including tendency to shoal and school. Individual sociability, often measured with a shoal choice assay (Cooper et al., 2018; Killen, Nadler, et al., 2021; Pilakouta et al., 2023), refers to the tendency of individuals to associate with other individuals, usually conspecifics.

While sociability of individuals in a group may itself impact shoal dynamics (Bevan et al., 2018; Jolles et al., 2017), sociability is also often linked to other behavioural traits displayed at the individual level. These include activity level, and risk-taking or exploratory behaviour (Conrad et al., 2011; Harcourt et al., 2009; Pike et al., 2008). Risk-taking behaviour is used here to refer broadly to the tendency of individuals to put themselves in situations that may have direct negative survival or fitness consequences, such as situations that increase predation risk (Huntingford et al., 2010; Koets et al., 2025). Risky behaviours may thus include leaving a shelter, approaching a novel object, or spending time in an open environment (Huntingford et al., 2010; Toms et al., 2010) and may describe exploratory behaviour if this involves time spent in the open or away from a shoal (Aich et al., 2025). Risk-taking is therefore sometimes considered antithetical to sociability, and various studies have indeed found the two to be negatively correlated in fish (Conrad et al., 2011; Harcourt et al., 2009; Pike et al., 2008).

Similarly, activity level may impact the tendency for fish to be social, with more active individuals sometimes being found to have a greater tendency to leave a shoal (Bartolini et al., 2015). Disparity in preferred or optimum swimming speed may also cause fragmentation of shoals into smaller groups (Killen, Marras, et al., 2017). It is important to note, however, that interactions among behavioural traits flow in all directions, and the social environment may also impact activity level (Tiddy et al., 2025) and tendency to risk-taking in fish (Harcourt et al., 2009). Suites of correlated traits displayed by individual fish are sometimes referred to as behavioural syndromes (Conrad et al., 2011), and the effects of individual behavioural traits on group dynamics are modulated by the expression of

other traits (Harcourt et al., 2009; Jolles et al., 2017). Understanding of the impacts of interindividual variation in behavioural traits or syndromes on group dynamics in fish is limited (Jolles, King, et al., 2020), however, as is understanding of the impacts of intraindividual variation across life stages or gradients of abiotic factors (Killen, Cortese, et al., 2021).

1.2.3. *Linking individual and group dynamics across contexts*

The effects of individual behavioural traits on group dynamics in fish are increasingly recognised as requiring study, particularly as existing studies have shown links among behaviours displayed across social contexts to be anything but simple (Jolles et al., 2017; Killen et al., 2026). The majority of studies linking individual behavioural traits with group dynamics have done so using very small groups of 2-3 individuals (Bevan et al., 2018; Harcourt et al., 2009; Nakayama et al., 2012, 2016; Riley et al., 2025), and while these provide valuable data, the social context is markedly different to that experienced in larger groups (Fu, 2016; Killen et al., 2026). Obtaining data for identified fish with known individual traits in group settings is logistically challenging, requiring high-resolution tracking and significant time investment to ensure individuals are accurately tracked (Jolles et al., 2017). Such studies have shown, however, that individual traits do indeed impact group dynamics. A study by Jolles et al. (2017) found that stickleback *Gasterosteus aculeatus* displaying greater risk-taking behaviour when alone were more likely to lead when in groups of five, but only where these individuals also showed low sociability in shoal choice assays (Jolles et al., 2017). Studies on smaller groups have found that risk-taking is also associated with leadership and decision-making in *G. aculeatus* pairs (Bevan et al., 2018; Harcourt et al., 2009; Nakayama et al., 2012; Riley et al., 2025) and trios (Nakayama et al., 2016). A key remaining question, however, is whether intraindividual variation in behavioural traits measured independently of conspecifics may be linked to variation in the roles of said individuals when in a group.

While individual fish often show strong repeatability in behavioural traits under a given set of conditions (Jolles et al., 2017; Villegas-Ríos et al., 2017), changes in ontogeny (Cabrera et al., 2021; Polverino et al., 2016), social context (Killen et al., 2026; Tiddy et al., 2025), and environmental variables (Killen, Cortese, et al., 2021) may alter trait expression. For example, in a species for which co-occurring high risk-taking and low sociability is correlated with group leadership, as found in Jolles et al. (2017), an individual displaying high risk-taking behaviour but low sociability as a juvenile may tend to lead groups during

that life stage. If that individual maintains high risk-taking behaviour but becomes more social as an adult, however, the correlation between risk-taking and group leadership may disappear if increased sociability leads to a change in shoaling dynamics (Bevan et al., 2018). As the magnitude of variation in behavioural traits across contexts is likely to differ among individuals (Killen, Adriaenssens, et al., 2016; Killen, Cortese, et al., 2021), considering variation itself as a trait may be key in determining the role of individuals across contexts. Intraindividual behavioural repeatability may vary across contexts (Killen, Adriaenssens, et al., 2016), while at the interindividual level, stressors can reduce variation within the population by homogenizing traits among individuals (Tan et al., 2020) (Figure 1.1). A thorough understanding of the effects of individual traits on group dynamics across contexts therefore depends on interpreting the influence of both inter- and intraindividual variation (Andreassen et al., 2026; Killen, Adriaenssens, et al., 2016; Stamps et al., 2012).

1.3. Modification of social behaviour in the context of stressors

While the relationships between individual traits and group dynamics, particularly in the context of stressors, still require elucidation, disruption or modification of social behaviour across contexts may occur through a number of avenues (Michelangeli et al., 2022).

Increases in metabolic rate, such as those observed under high temperatures or in response to certain chemical pollutants, are often associated with increases in activity level that may cause shoals to fragment (Davis et al., 2019; Killen, Marras, et al., 2017) or reduce cohesion (Armstrong et al., 2019; Bartolini et al., 2015; Davis et al., 2019). Increased metabolic needs may also shift individual prioritisation of social behaviour (Ioannou, 2017; Killen, Cortese, et al., 2021). Specifically, while group foraging is associated with greater ability to locate food patches (Pitcher et al., 1982), this food must be shared with groupmates. Increasing food requirements may therefore incentivise individuals to leave shoals, to increase foraging time and avoid sharing (Ioannou, 2017; Killen, Cortese, et al., 2021). Pollutants such as antidepressants may reduce anxiety or stress, leading to individuals straying from shoals as risk-taking increases (Maulvault et al., 2018; Salahinejad et al., 2022). Conversely, alarm caused by acute exposure to noise or light pollution may cause fish to move closer together (Neo, Parie, et al., 2015; Neo, Ufkes, et al., 2015), while longer-term stress from these factors may lead to increased metabolic costs and associated changes in risk-taking behaviour, activity, and sociability (Georgiou et al., 2024; Kurvers et al., 2018). Interference with cognitive function or sensory pathways due to chemical pollutants, hypoxia, or acidification may lead to reduced cohesion as the rapid responses required for shoaling and schooling are impaired (Michelangeli et al.,

2022). Whatever the mechanism, disruptions to social behaviour could have significant ecological ramifications, including impacts on predation risk, fitness, foraging, mate-finding, and survivorship (Pitcher, 1986; Pitcher et al., 1982; A. Ward & Webster, 2016b, 2016a). Elucidating the effects of anthropogenic stressors on fish behaviour across social contexts is therefore a key concern for understanding how fish may respond to environmental change, however the diversity of stressors, fish species, and the behaviours themselves often make studies challenging.

1.4. Challenges associated with studies of the effects of anthropogenic stressors on fish social behaviour

1.4.1. Studies of the effects of climate-related stressors

Identifying unifying trends regarding the impact of climate-related stressors such as temperature, acidification, and hypoxia on fish behaviour is further complicated by the diversity of fish and of the environments they inhabit. The physiological vulnerability, and therefore the magnitude of behavioural response, to a given change in temperature, for example, may vary significantly among niches, species, populations (Jutfelt, 2020; A. Mitchell et al., 2022), and individuals (Killen et al., 2012). A well-studied example of this is sympatric stickleback populations inhabiting Icelandic lakes, some of which are heated by thermal springs (Jutfelt, 2020). These populations show significant variation in metabolic response to temperature change, even within a species and geographical region (Pilakouta et al., 2020). Findings concerning thermal tolerance may therefore have relatively low potential for generalisation across contexts.

Difficulty in integrating findings is increased as, even assuming similar physiological vulnerability, behavioural strategies for coping with abiotic stressors also vary among species. Activity responses to hypoxia, for example, often fall into two distinct but entirely opposite categories (Domenici et al., 2017). Some studies show reduced activity in response to hypoxia, likely associated with attempts to conserve oxygen (Alfonso et al., 2020; Cook et al., 2014; Hayes et al., 2019). Others have found increased activity, possibly due to attempts to escape unfavourable conditions (Domenici et al., 2000; Sommer-Trembo et al., 2017). Fish shoals have often been found to reduce cohesion under hypoxic conditions, as proximity to conspecifics equates to competition for oxygen (Domenici et al., 2017), though some species may be able to avoid this by reducing swimming speed

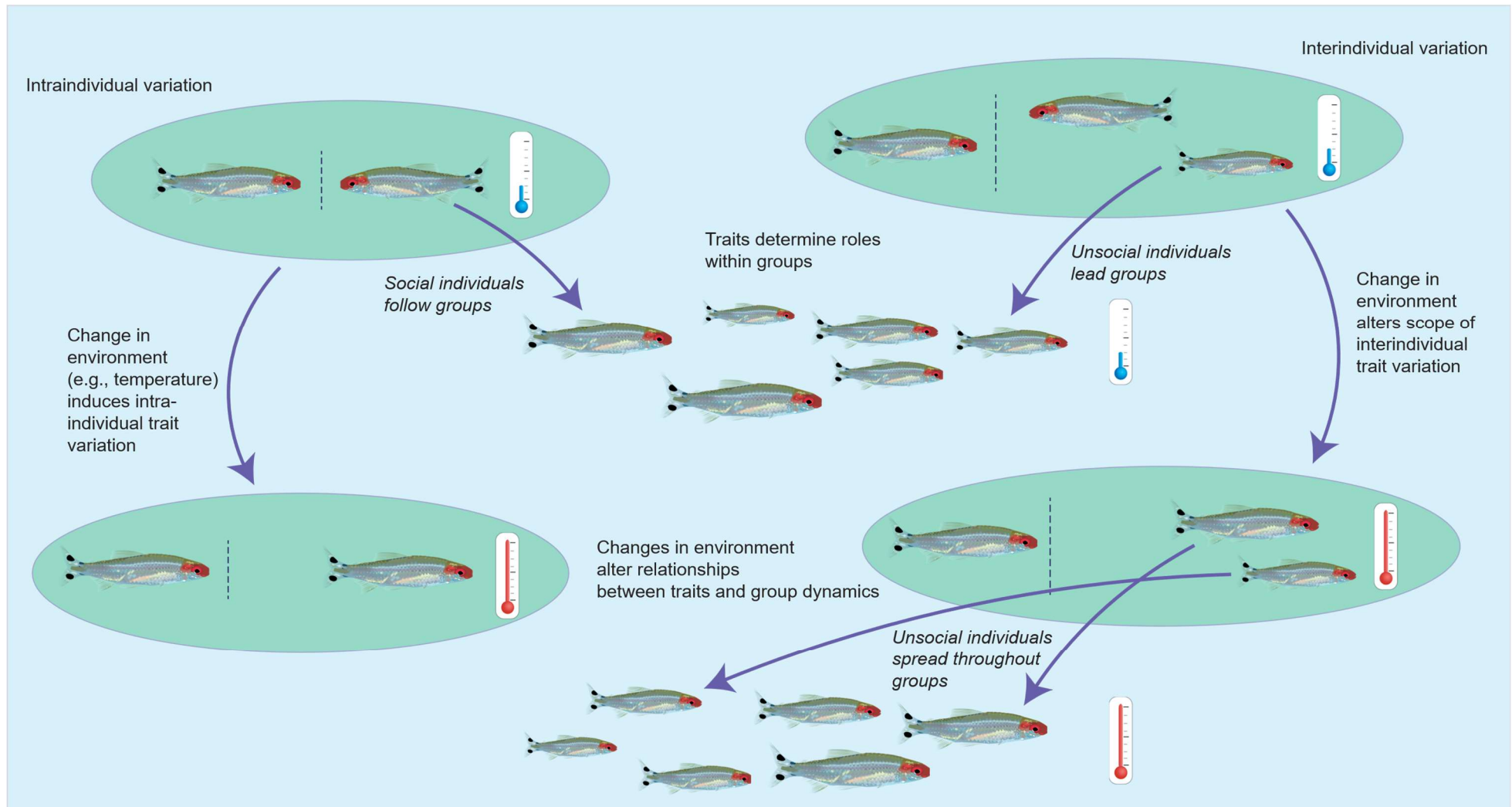


Figure 1.1. Theoretical effects of inter- and intraindividual variation in behaviour with environmental context on shoaling dynamics

(Cook et al., 2014; Domenici et al., 2002). Specialised behavioural adaptations to hypoxia, such as air breathing or surface skimming, may allow fish to tolerate hypoxia (Obirikorang, Viala, et al., 2025; Pineda et al., 2020) but are often linked to risk-taking, as surfacing increases vulnerability to terrestrial or aerial predators (Obirikorang, Yussif, et al., 2025). Stressors such as hypoxia and acidification may have greater effects on marine compared with freshwater species, as the magnitude of natural variation in these factors is low in the marine environment (Ishimatsu et al., 2004; Kwong et al., 2014). As many model fish species, such as stickleback and zebrafish *Danio rerio*, are freshwater, however, marine species may be underrepresented in the literature.

An additional dimension is that climate-related stressors, as discussed above, often occur together (Nagelkerken & Connell, 2015; Shivanna, 2020, 2022). Studies of these factors must therefore contend with variation at the intra- and interindividual levels, the taxonomic level, and with reference to the evolutionary and developmental environment of the study organisms, all while balancing the scientific need for controlled comparative levels with ecological realism and relevance. All of these factors mean that there is some uncertainty associated with the state of the literature and unifying themes present therein in the field of fish social behaviour in the context of climate-related stressors.

1.4.2. *Studies of the effects of anthropogenic pollutants*

Some similar challenges are present with studies of chemical pollutants, though another major issue with these studies is the diversity of substances that are present in aquatic environments as pollutants (Orr et al., 2024; Zhang et al., 2023). While substances can sometimes operate through similar metabolic pathways (Bertram, Gore, et al., 2022; Escher et al., 2011), generalisation is still challenging due to variation in effect doses, bioavailability, and toxicity of secondary metabolites (Michelangeli et al., 2022), as well as interactions with other stressors (Bertram, Martin, et al., 2022b). The majority of contaminated waterways contain more than one foreign substance (Alfonso et al., 2022; Cervený et al., 2020; Orr et al., 2024), magnifying the challenges associated with ascertaining ecologically relevant effects of a specific substance, and increasing the need to understand effects of substances in combination (Zhang et al., 2023). Even if substances do not have interactive metabolic effects, the presence of certain substances may modulate the ability of organisms to cope with others (Orr et al., 2024). For example, adsorption, the process of a substance adhering to the surface of another particle, often a microplastic particle, can increase both the bioavailability of substances in an environment and their

pervasiveness across systems (Chen et al., 2022; Santos et al., 2020, 2021; Zhang et al., 2023). As ALAN and noise pollution also increasingly permeate into aquatic environments (Davies et al., 2014; Marangoni et al., 2022), the chances that these will appear alongside forms of chemical pollutant are likewise amplified.

The diurnal effects of ALAN in particular are understudied, as previous research has reasonably focused on nocturnal behavioural alterations in species and systems exposed to artificial light (Georgiou et al., 2024). Other studies have examined the effects of visual disturbances and variance in light levels during testing, rather than the effects of ALAN exposure *per se* (Chaput et al., 2023; Matchette & Herbert-Read, 2021; J. Zhao et al., 2020). Changes to diurnal behaviours in ALAN-exposed fish have been found, however, likely associated with chronic disruption of melatonin production, the hormone associated with sleep and maintaining circadian rhythms (Gaston & Sánchez de Miguel, 2022; Grubisic et al., 2019). It has been theorised that disruption to natural cycles of melatonin production and therefore natural sleep cycles may cause overactivation of stress responses in ALAN-exposed fish species, similar to the effects observed in populations subject to high predation (Kurvers et al., 2018). This has the potential to alter diurnal behaviours including activity, risk-taking, and sociability (Kurvers et al., 2018). The effects of ALAN on daytime behaviour remain poorly understood, however, and no comprehensive synthesis of the literature currently exists regarding the effects on fish social behaviour of ALAN or other forms of pollution.

1.5. Thesis aims and overview

Although a number of studies exist on the effects of both climate-related stressors (see Chapter 2) and anthropogenic pollution (see Chapter 3) on social behaviour in fish, the state of the literature remains in places uncertain. The increasing ubiquity and severity of exposure to anthropogenic stressors in aquatic ecosystems highlights the urgent need for both an improved understanding of the current state of the literature, and for further empirical studies targeting key knowledge gaps. Studies linking individual behavioural traits with group dynamics are notably lacking, with only one study to date (Jolles et al. 2017) quantifying the role of individuals with known traits in multi-individual shoals of fish. While various studies have found effects of anthropogenic stressors on both behaviour displayed independently from conspecifics and behaviour in a shoal, relatively few have measured both in the same system (but see Table 2.3, Supplementary Table 3.1). Further, studies linking behaviour when alone with behaviour in a group in the context of these

stressors are entirely absent from the literature. This lack of data on the role of intra- and interindividual variation in determining group responses to stressors may lead to key interactions and effects of social context being missed (Killen et al., 2026). While in gregarious species, ecological interactions may often occur at the level of the group (Michelangeli et al., 2022), the physiological impact of environmental stressors and thus the initial behavioural response occurs at the level of the individual (Killen, Cortese, et al., 2021). Individual behavioural responses, their modifiers, and their role in determining group dynamics are therefore essential to understanding how environmental change may affect behaviour in gregarious fish species (Jolles et al., 2018; Killen et al., 2026).

Gaps in the literature are also apparent in the case of some specific stressors, most notably artificial light at night, the effects of which on diurnal sociability in fish had been quantified by only one study (Kurvers et al., 2018) prior to the writing of this thesis. As an increasingly common stressor (Davies et al., 2014; Kyba et al., 2023; Marangoni et al., 2022), ALAN is of rising concern to ecologists working across systems, and the lack of data on fish species should be a key focus point. This thesis aims to systematically assess the current state of the literature surrounding the impacts of anthropogenic stressors on social behaviours in gregarious fish. Chapters 2 and 3 therefore consist of systematic meta-analyses investigating the effects of climate-related stressors and anthropogenic pollutants respectively. I further aim to address key knowledge gaps by studying whether climate-related stressors modulate relationships between individual behavioural traits and group dynamics, and by obtaining empirical data on the effects of artificial light at night, an understudied stressor, on diurnal sociability and related behaviours. Specifically, chapters 4 and 5 use tracking of individual fish with known traits to investigate the effects of thermal stress and hypoxia respectively on group dynamics and the role of individuals in shoals. Chapter 6 studies the effects of wild, chronic exposure to ALAN on diurnal sociability, activity, and risk-taking behaviour in a gregarious fish.

1.5.1. Chapter 2: Impacts of climate-related stressors on social group cohesion and individual sociability in fish

In this review, I conducted a systematic meta-analysis of the current literature pertaining to the effects of climate-related stressors, specifically temperature, hypoxia, and acidification, on shoaling and schooling behaviour (group cohesion) and individual sociability in fish. The existing literature was reviewed up to early 2023, and available data on treatment,

assayed behavioural metrics, fish species, location of studies, and observed effect sizes was collected for each of 45 relevant studies.

1.5.2. Chapter 3: Impacts of anthropogenic pollutants on social group cohesion and individual sociability in fish: A systematic review and meta-analysis

Here, I review the current literature on the effects of chemical pollutants, noise pollution, and light pollution on group cohesion and individual social behaviour in fish. Papers published up to 2023 were screened, and a total of 165 studies selected for inclusion. Data on treatment, pollutant class, fish species, assayed behavioural metrics, location of studies, and observed effect sizes was collected where available. Studies for which sufficient data could be obtained ($n = 141$) were included in meta-analysis to identify trends across the literature.

1.5.3. Chapter 4: Changes to group dynamics reflect changes in individual behaviour under thermal stress in a model fish species

In this experiment, I investigate the effects of short-term thermal stress on individual behavioural traits, namely sociability, activity, and risk-taking behaviour, in a model species, rummy-nose tetra *Hemigrammus rhodostomus*. Behavioural traits were assayed at three temperatures representing close to the full range of temperatures experienced by this species in the wild. I further test the response of groups of *H. rhodostomus* to the same thermal treatments at both the group and individual levels and assess the impacts of temperature on the roles and dynamics of individuals with known traits in groups.

1.5.4. Chapter 5: Hypoxia alters the link between individual behavioural variation and collective dynamics in a social fish

In a parallel experiment to that described in Chapter 4, I study how exposure to hypoxia affects social behaviour when alone and in groups in *H. rhodostomus*. Behavioural trials were carried out under normoxia (i.e., full oxygen air saturation), mild hypoxia (70% O₂), and severe hypoxia (30% O₂). I further analyse the independent and interactive effects of oxygen level and traits of individuals within groups on group dynamics.

1.5.5. Chapter 6: Effects of artificial light at night on the diurnal risk-taking behaviour of a gregarious reef fish

This experiment sought to elucidate the effects of chronic exposure to artificial light at night (ALAN) in the wild on sociability, activity, and risk-taking behaviour (emergence from a shelter) in a gregarious reef fish, threespot dascyllus *Dascyllus trimaculatus*. Fish were exposed in the wild to either ambient light levels or ALAN from the time of settlement. Sociability and activity were measured before and after a chase stimulus. Time and tendency to emerge from an anemone, and distance to the anemone, following said chase stimulus were also quantified.

1.6. Summary

Anthropogenic stressors, including climate-related abiotic factors, chemical pollutants, and non-chemical pollutants, are a near-ubiquitous feature of aquatic systems. Mobile species such as fish often respond behaviourally to non-lethal levels of anthropogenic stressors, improving short-term survival but potentially affecting normal ecological interactions. In gregarious species, impacts on social behaviour may be particularly relevant to survival and fitness, as social behaviour is a vital component of foraging, predator evasion, and reproduction for many species. While evidence of the effects of anthropogenic stressors on fish social behaviour is growing, the diversity of the stressors, environments, and species involved and the breadth of impacts across ecosystems makes it challenging to draw general conclusions. In addition, the multiple levels of among- and within-individual behavioural variation involved in social interactions make assessing links between effects of stressors at the individual level and emergent changes in group dynamics a challenging task. The component chapters of this thesis will therefore use a combination of literature-based and experimental approaches to identify and fill gaps in the literature on the topic of effects of anthropogenic stressors on fish social behaviour.

Chapter 2

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

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2.1. 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.

2.2. 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 et al., 2021; Domenici et al., 2013; Heuer & Grosell, 2014). 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 CO₂ 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 et al., 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 (Diaz & Rosenberg, 2008; Nagelkerken & Connell, 2015).

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 (Clarke & Johnston, 1999; Nati et al., 2018; Pilakouta et al., 2020). Hypoxia and elevated CO₂ 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 (Killen, Marras, et al., 2017; Metcalfe et al., 2016). 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, Marras, 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) (N. Miller & Gerlai, 2012; Palacios-Fuentes et al., 2020) 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 [Click or tap here to enter text.](#) (Killen, Fu, et al., 2016; Pilakouta et al., 2023; Webster & Hart, 2006). Warming or hypoxia can also alter individual activity (Bartolini et al., 2015; Lefrançois 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 (Angiulli et al., 2020; Cooper et al., 2018). The effects of temperature, hypoxia, and acidification may also affect neurological functioning (Andreassen et al., 2022; Toni et al., 2019; Topal et al., 2021), and sensory systems (McKee et al., 2020), directly affecting the mechanisms by which fish can sense conspecifics and coordinate behaviours with groupmates (Corral-Lopez et al., 2023; McKee et al., 2020) and potentially disrupting

group functioning (Killen, Cortese, 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 et al., 2000; Pineda et al., 2020). Increased environmental and systemic carbon dioxide partial pressure ($p\text{CO}_2$) corresponds to reduced pH (acidification) of water. To maintain blood pH under high $p\text{CO}_2$ 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; A. Mitchell et al., 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.

2.3. Methods

2.3.1. 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 (Figure 2.1; Table 2.1).

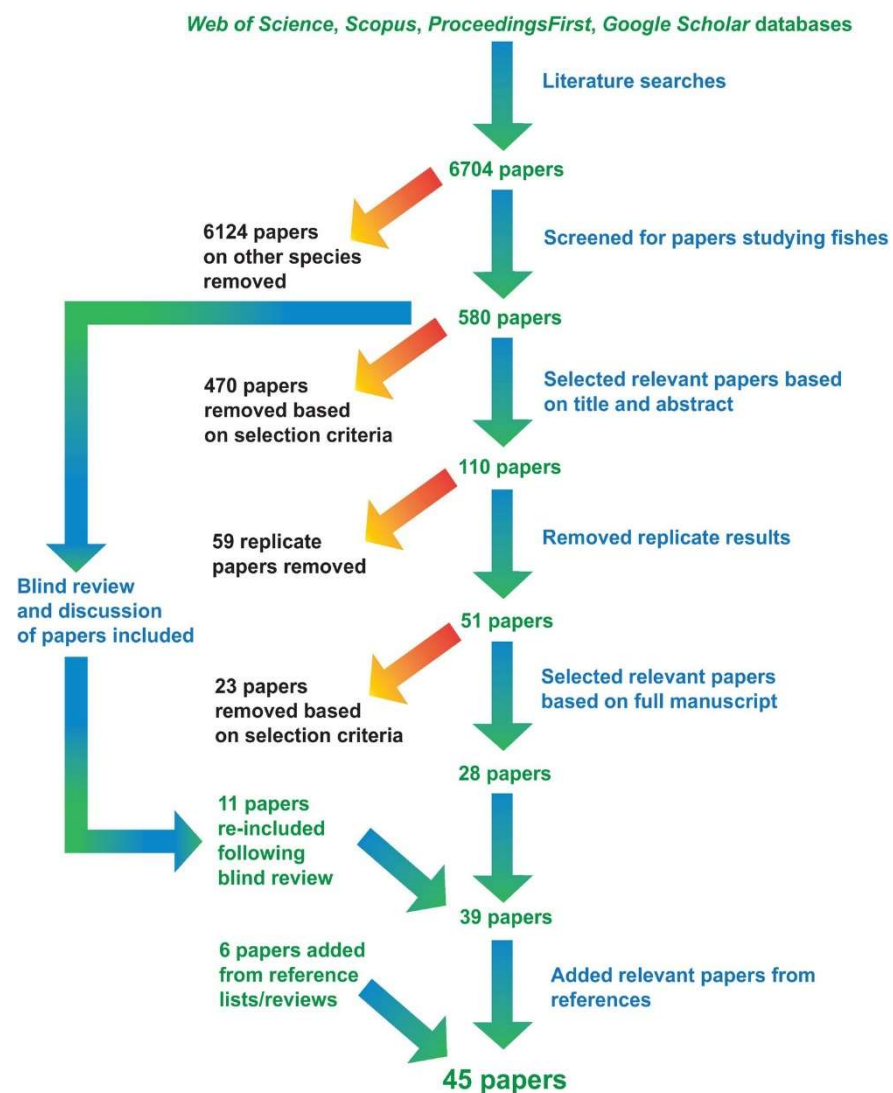


Figure 2.1. Flow diagram illustrating paper selection process for systematic review.

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 2.1). A further six relevant studies were identified from references in studies found from searches (Figure 2.1). 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.

Table 2.1. Search terms and sources used to find papers included in this review.

Database	Search term	Results	Results examined	Results included in analysis
<i>Web of Science</i>	temperature AND "social* behaviour"	2,669	All	23
<i>Web of Science</i>	hypoxia AND "social* behaviour"	76	All	1
<i>Web of Science</i>	temperature AND "group cohesion"	15	All	0
<i>Web of Science</i>	hypoxia AND "group cohesion"	5	All	0
<i>Web of Science</i>	temperature AND "sociability"	84	All	3
<i>Web of Science</i>	hypoxia AND "sociability"	10	All	0
<i>Web of Science</i>	acidity AND "social* behaviour"	13	All	1

<i>Web of Science</i>	acidity AND "group cohesion"	0	All	0
<i>Web of Science</i>	acidity AND "sociability"	3	All	0
<i>Web of Science</i>	acidification AND "social* behaviour"	33	All	3
<i>Web of Science</i>	acidification AND "group cohesion"	3	All	0
<i>Web of Science</i>	acidification AND sociability	0	All	0
<i>Scopus</i>	temperature AND "social* behaviour"	1238	All	1
<i>Scopus</i>	hypoxia AND "social* behaviour"	102	All	0
<i>Scopus</i>	temperature AND "group cohesion"	12	All	0
<i>Scopus</i>	hypoxia AND "group cohesion"	2	All	0
<i>Scopus</i>	temperature AND "sociability"	57	All	0
<i>Scopus</i>	hypoxia AND "sociability"	7	All	0
<i>Scopus</i>	acidity AND "social* behaviour"	11	All	0
<i>Scopus</i>	acidity AND "group cohesion"	0	All	0
<i>Scopus</i>	acidity AND "sociability"	1	All	0
<i>Scopus</i>	acidification AND "social* behaviour"	9	All	0
<i>Scopus</i>	acidification AND "group cohesion"	2	All	0
<i>Scopus</i>	acidification AND sociability	1	All	0
<i>ProceedingsFirst</i>	temperature AND "social* behaviour"	101	All	0
<i>ProceedingsFirst</i>	hypoxia AND "social* behaviour"	13	All	0
<i>ProceedingsFirst</i>	temperature AND "group cohesion"	7	All	0
<i>ProceedingsFirst</i>	hypoxia AND "group cohesion"	2	All	0
<i>ProceedingsFirst</i>	temperature AND "sociability"	20	All	0
<i>ProceedingsFirst</i>	hypoxia AND "sociability"	1	All	0
<i>ProceedingsFirst</i>	acidity AND "social* behaviour"	1	All	0
<i>ProceedingsFirst</i>	acidity AND "group cohesion"	0	All	0
<i>ProceedingsFirst</i>	acidity AND "sociability"	0	All	0
<i>ProceedingsFirst</i>	acidification AND "social* behaviour"	3	All	0
<i>ProceedingsFirst</i>	acidification AND "group cohesion"	0	All	0
<i>ProceedingsFirst</i>	acidification AND sociability	3	All	0
<i>Google Scholar</i>	effects of temperature on social behaviour in fish	485000	Top 100 by relevance	1
<i>Google Scholar</i>	effects of temperature on group cohesion in fish	91100	Top 100 by relevance	2
<i>Google Scholar</i>	effects of temperature on sociability in fish	21500	Top 100 by relevance	0
<i>Google Scholar</i>	effects of hypoxia on social behaviour in fish	26400	Top 100 by relevance	0
<i>Google Scholar</i>	effects of hypoxia on group cohesion in fish	19900	Top 100 by relevance	1
<i>Google Scholar</i>	effects of hypoxia on sociability in fish	1860	Top 100 by relevance	2

<i>Google Scholar</i>	effects of acidity on social behaviour in fish	30600	Top 100 by relevance	0
<i>Google Scholar</i>	effects of acidity on group cohesion in fish	21100	Top 100 by relevance	0
<i>Google Scholar</i>	effects of acidity on sociability in fish	1430	Top 100 by relevance	0
<i>Google Scholar</i>	effects of acidification on social behaviour in fish	32800	Top 100 by relevance	0
<i>Google Scholar</i>	effects of acidification on group cohesion in fish	22300	Top 100 by relevance	0
<i>Google Scholar</i>	effects of acidification on sociability in fish	1360	Top 100 by relevance	0

2.3.2. 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 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 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; Fahlman et al., 2021; Israeli & Kimmel, 1996; Mameri et al., 2020; O'Driscoll & McClatchie, 1998; Olla et al., 1985; Palacios-Fuentes et al., 2020; Stienessen, 2015; 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., 2016; 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.

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

Equation 1.1.
$$Cd = \frac{\bar{x}_1 - \bar{x}_2}{PSD}$$

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

Equation 1.2.
$$PSD = \sqrt{\frac{N^1 - 1SD_1^2 + N^2 - 1SD_2^2}{N^1 + N^2 - 2}}$$

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:

Equation 1.3.
$$Hg = 1 - \frac{3}{4 \times N^1 + N^2 - 9} \times Cd$$

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

Equation 1.4.
$$\sigma = SE\sqrt{N}$$

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:

Equation 1.5.
$$\sigma = \frac{\sqrt{N} \times upper\ limit - lower\ limit}{3.92}$$

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 et al., 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 et al., 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 et al., 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) 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 2.2). 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 2.2). 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 2.2). 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.

Table 2.2. Metrics used in studies included in this review to measure group cohesion or sociability. 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.

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	1 st , 2 nd , 3 rd 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	

2.3.3. 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 (Guillermé & 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.

2.4. Results

2.4.1. 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 2.3), of which 347 data points from 36 studies were included in the meta-analysis (Figure 2.2A). 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 (Figure 2.3). No studies were carried out in Africa. A total of 43 species were utilised in studies (Figure 2.4), with no particular bias towards any species or group, although marine species were more commonly used than freshwater or estuarine/anadromous species (Figure 2.5A). The most popular species was the three-spined stickleback *Gasterosteus aculeatus* L. 1758, which was used in four studies (Figure 2.4). Exposure period to stressors ranged from <10 min to 300 days (Figure 2.5B). 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 (Figure 2.2B). This may be due to a publication bias against studies with small sample sizes that reported either null results or positive results. There was a minimal phylogenetic signal across studies ($\lambda = 0.101$; $p = 0.241$).

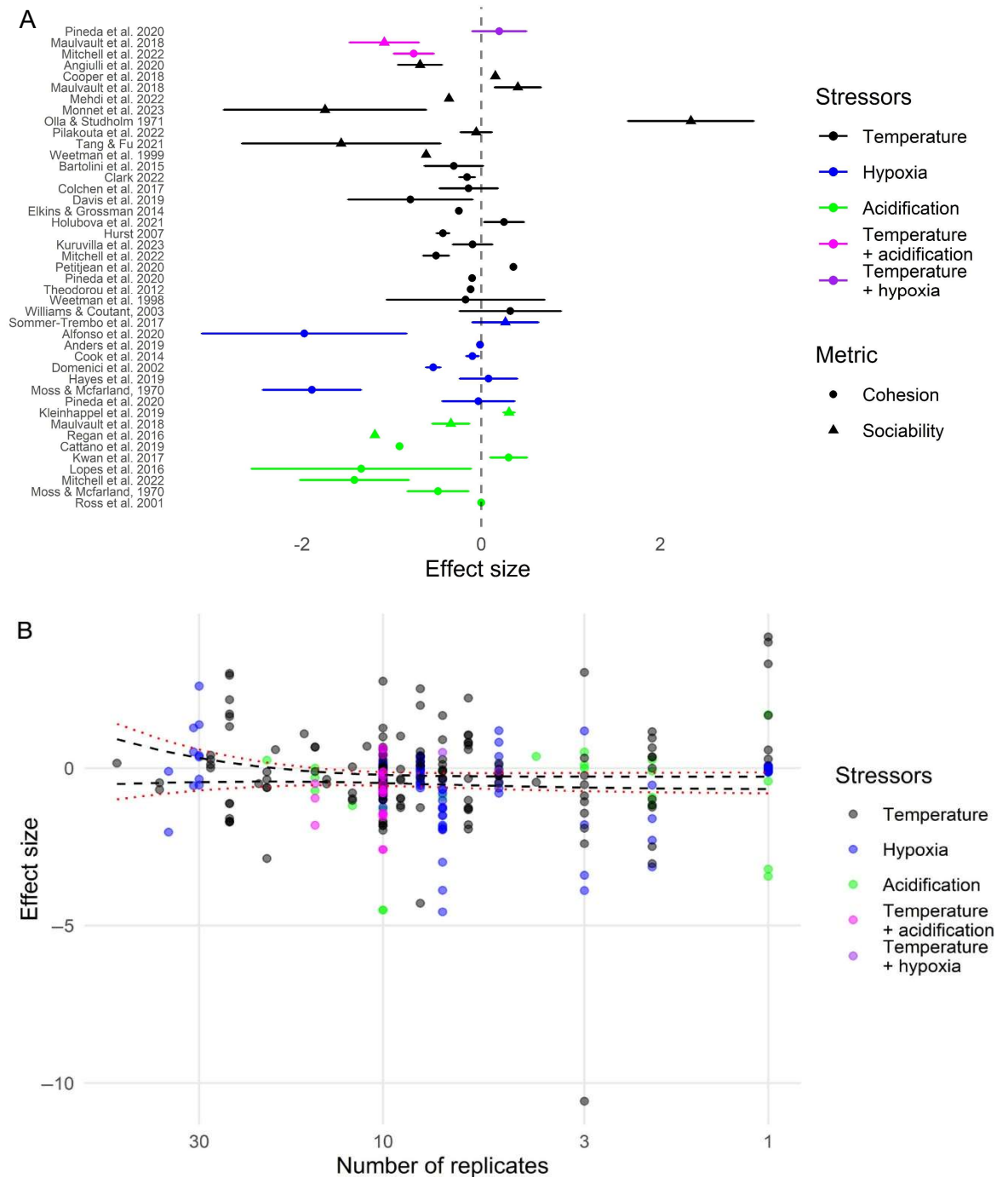


Figure 2.2A. Forest plot showing mean effect sizes (Hedges' g) of climate stressors on group cohesion and sociability in fishes. Mean and standard error of effect size for each study was calculated from effect sizes calculated for all treatment levels. **B.** Funnel plot showing effect size plotted against 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.



Figure 2.3. 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.

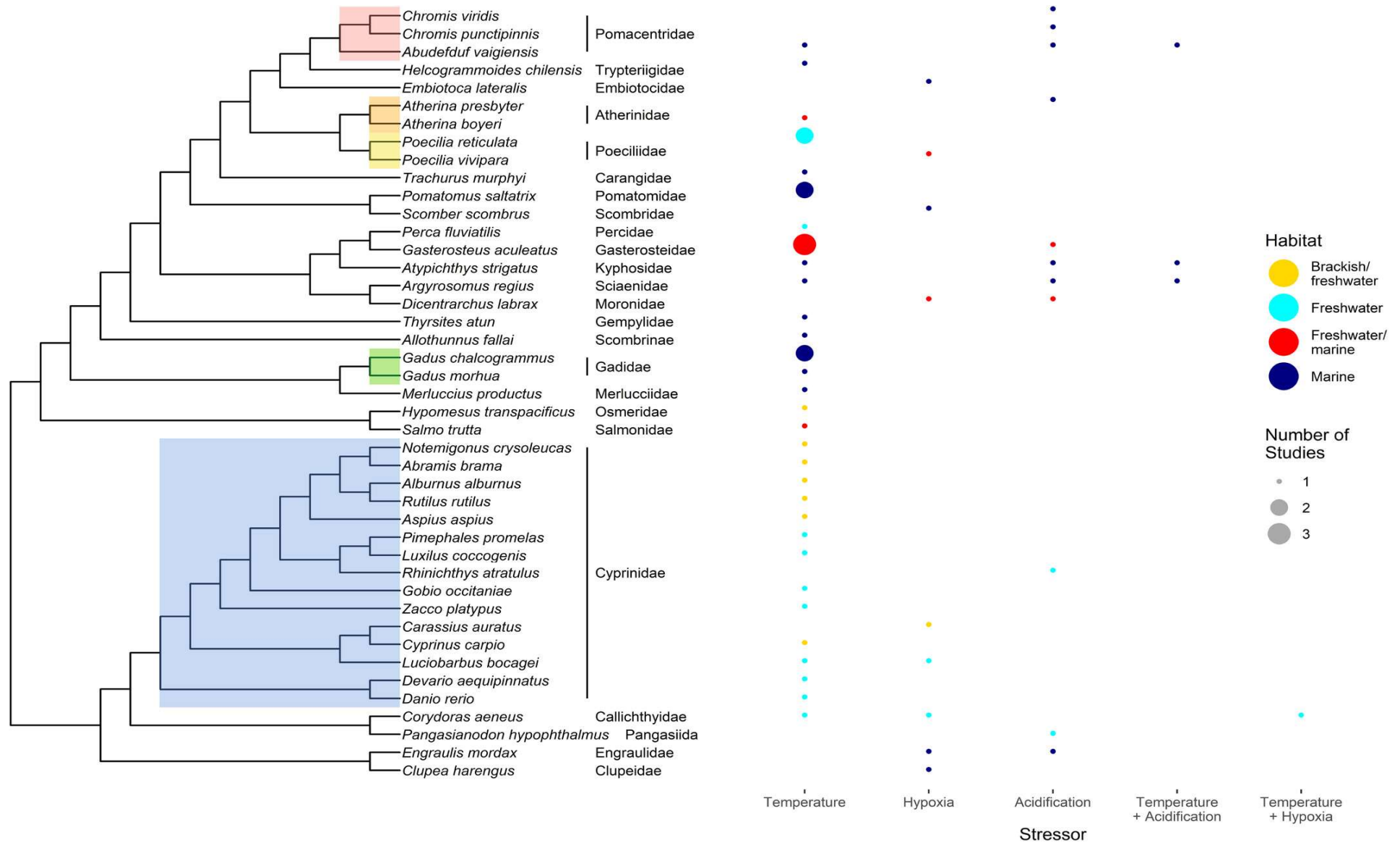


Figure 2.4. Dendrogram showing species and families (coloured where multiple species are present in a family) included in the meta-analysis, with dot plot showing stressors studied for each species and the number of studies carried out on each species. Species habitat is indicated by dot colour.

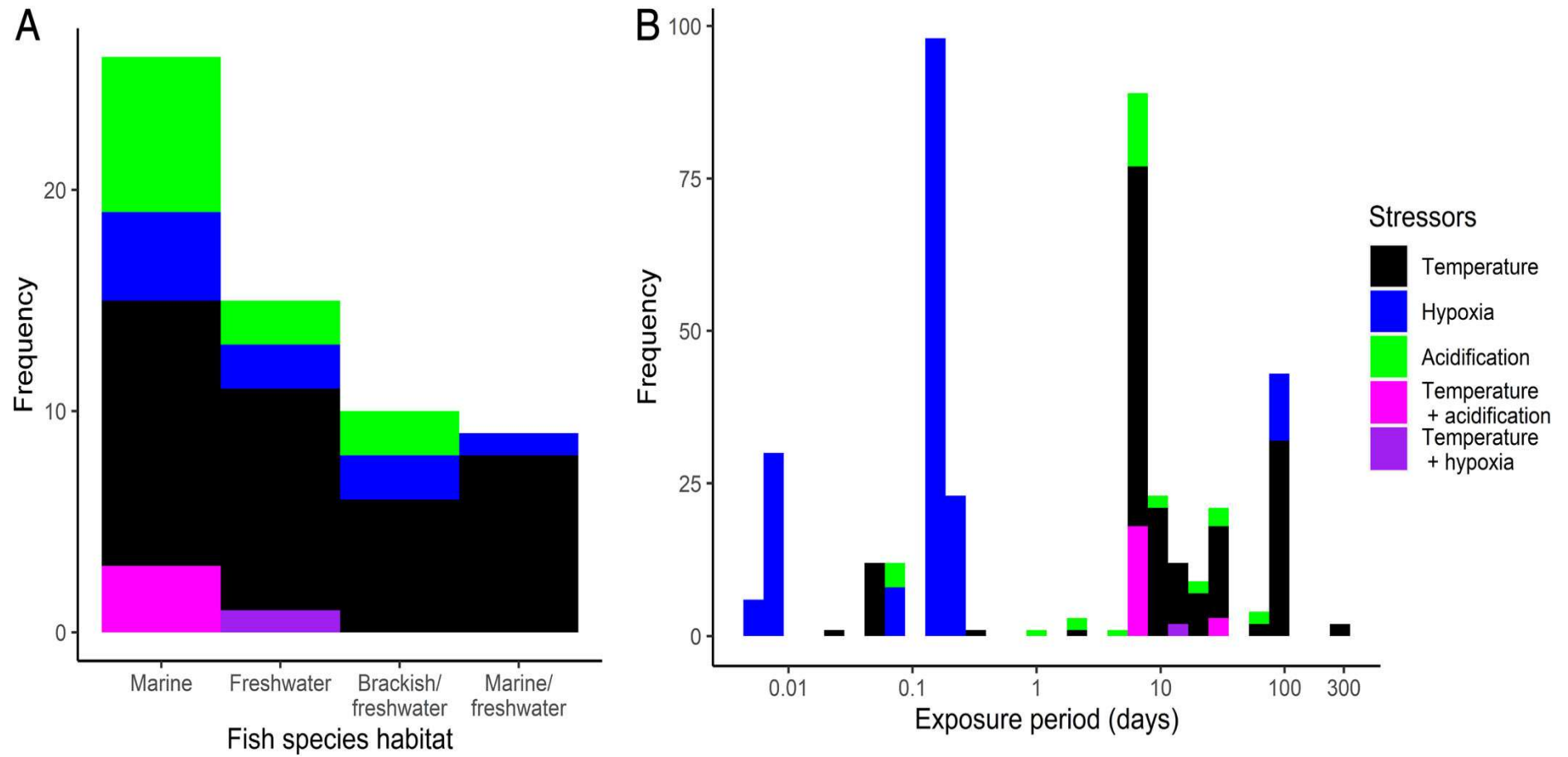


Figure 2.5. Frequency histograms of A. species included in all studies in our database according to their habitat, and B. exposure periods and stressors used in all studies included in our database.

Table 2.3. Summary of all studies included in this review. ‘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 Figure 2.2A. + 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.

Climate variable	Metric	Reference	Species	Treatments	Exposure period	Reported results	Results summary (mean effect size)
	Sociability	Angiulli <i>et al.</i> (2020)	<i>Danio rerio</i>	26 °C, 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 <i>et al.</i> (2018)	<i>Gasterosteus aculeatus</i>	Increasing or decreasing temperature	30 min; acute	Stronger association with shoal when shoal was located in a cool environment	+
		Maulvault <i>et al.</i> (2018)	<i>Argyrosomus regius</i>	19 °C, 24 °C	28 days; acclimated	Increased time near conspecifics. No effect on latency of approach or number of approaches.	+
		Mehdi <i>et al.</i> (2022)	<i>Pimephales promelas</i>	4 °C, 20 °C	21 days; acclimated	No effect on time near or time spent interacting with a conspecific	–
		Monnet <i>et al.</i> (2023)	<i>Salmo trutta</i>	12.41 °C, 12.72 °C, 15.02 °C	100 days; uncontrolled	No effect on sociability score	–
		Pilakouta <i>et al.</i> (2022)	<i>Gasterosteus aculeatus</i>	10 °C, 12 °C, 18 °C	30 days; acclimated	No effect on distance to conspecific shoal in parental generation, increased distance in F2	0
		Tang & Fu (2021)	<i>Zacco platypus</i>	21.7 °C, 25.6 °C, 26.23 °C, 27.3 °C, 28.73 °C, 29.07 °C	100 days; uncontrolled	No effect of temperature on sociability score	–
		Weetman <i>et al.</i> (1999)	<i>Poecilia reticulata</i>	22 °C, 26 °C	28 days; acclimated	No effect on shoal size choice	–
		Bartolini <i>et al.</i> (2015)	<i>Devario aequipinnatus</i>	22 °C, 25 °C, 28 °C	15 days; acclimated	Increased polarity at 25 °C, no effect on NND	0
		Clark (2022) (thesis)	<i>Gasterosteus aculeatus</i>	13.4 °C, 14.7 °C, 16.3 °C, 16.5 °C	100 days; uncontrolled	Reduced aggregation (used as a proxy for shoaling)	–

	Group cohesion	Colchen <i>et al.</i> (2017)	<i>Salmo trutta</i>	4 °C, 6 °C, 8 °C, 10 °C, 12 °C	9 days; acclimated	Increased NND at 8 °C and 10 °C, increased IID at 10 °C <i>versus</i> 6 °C, reduced physical contacts and variance in IID at 6 °C and 8 °C, increased approach-withdrawal frequency at 12 °C	0
		Davis <i>et al.</i> (2019)	<i>Hypomesus transpacificus</i>	17.1 °C, 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)	<i>Luxilus coccogenis</i>	12 °C, 17 °C	2 days; acute	Reduced group cohesion	–
		Fahlman <i>et al.</i> (2021)	<i>Perca fluviatilis</i>	Natural temperature fluctuations	14 days; uncontrolled	Reduced NND with increasing temperature	+ reported
		Holubova <i>et al.</i> (2021)	<i>Abramis brama</i> <i>Alburnus alburnus</i> <i>Cyprinus carpio</i> <i>Aspius aspius</i> <i>Perca fluviatilis</i> <i>Rutilus rutilus</i>	12 °C, 13 °C, 17 °C, 18 °C, 19 °C, 21 °C, 21.5 °C, 23 °C	100 days; uncontrolled	Increased group cohesion at higher temperatures	+
		Hurst (2007)	<i>Gadus chalcogramma</i> (<i>Theragra chalcogramma</i>)	2 °C, 5 °C, 9 °C	60 days; acclimated	Increased NND	–
		Kuruvilla <i>et al.</i> (2023)	<i>Notemigonus crysoleucas</i>	9 °C, 13 °C, 17 °C, 21 °C, 25 °C, 29 °C	7 days; acclimated	No effect on NND or convex hull area	0
		Mameri <i>et al.</i> (2020)	<i>Luciobarbus bocagei</i>	24.5 °C, 29.7 °C	9 h, repeated six times; acute	No effect on number of fish within 1 body length	No effect reported
		Mitchell <i>et al.</i> (2022)	<i>Abudefduf vaigiensis</i> <i>Atypichthys strigatus</i>	20 °C, 23 °C, 26 °C	6 days; acute	No effect on group cohesion	–
		O'Driscoll & McClatchie (1998)	<i>Allothunnus fallai</i> <i>Thyrsites atun</i> <i>Trachurus murphyi</i>	Natural temperature fluctuations	100 days; uncontrolled	No effect on horizontal school area	No effect reported

Temperature		Olla & Studholm (1971)	<i>Pomatomus saltatrix</i>	Increasing temperature (20–29 °C)	29–32 days; acclimated	Increased sociability index as temperature increases	+
		Olla <i>et al.</i> (1985)	<i>Pomatomus saltatrix</i>	1 °C, 14.8 °C, 19.1 °C	11 days (14.8 °C), 23 days (19.1 °C); acclimated	Reduced group cohesion	– reported
		Palacios-Fuentes <i>et al.</i> (2020)	<i>Helcogrammoides chilensis</i>	Natural temperature fluctuations	100 days; uncontrolled	More shoaling behaviour and fewer solitary individuals at higher temperatures. No effect on schooling behaviour.	+ reported
		Petitjean <i>et al.</i> (2020)	<i>Gobio occitaniae</i>	17 °C, 24 °C	30 days; acclimated	No effect on group cohesion score	+
		Pineda <i>et al.</i> (2020)	<i>Corydoras aeneus</i>	25 °C, 30 °C	14 days; acclimated	No effect on IID	–
		Steinessen (2015)	<i>Gadus chalcogramma</i> (<i>Theragra chalcogramma</i>)	Natural temperature fluctuations	100 days; uncontrolled	Reduced school density	– reported
		Swartzman (1997)	<i>Merluccius productus</i>	Natural temperature fluctuations	100 days; uncontrolled	Reduced group cohesion	– reported
		Theodorou <i>et al.</i> (2012)	<i>Gadus morhua</i>	3 °C, 13 °C	13 days; acclimated	No effect on IID	–
		Weetman <i>et al.</i> (1998)	<i>Poecilia reticulata</i>	22 °C, 26 °C	14 days; acclimated	Reduced NND and increased elective group size. No effect on polarity	0
		Williams & Coutant (2003)	<i>Atherina boyeri</i> (<i>Atherina mochon</i>)	20 °C, 28.5 °C	80 min during larval and/or egg stage; developmental	Increased approach-withdrawal frequency and latency to school formation. Reduced polarity and school duration	0
	Sociability	Sommer-Trembo <i>et al.</i> (2017)	<i>Poecilia vivipara</i>	Wild-caught fish from populations at 100%, ~88%, ~87%, ~71%, and ~47%	100 days; uncontrolled	No effect on time near conspecifics	0
	Group cohesion	Alfonso <i>et al.</i> (2020)	<i>Dicentrarchus labrax</i>	100%, 95%, 50%, 21% O ₂	90 min; acute	Increased IID at 21% SO ₂	–

Hypoxia		Anders <i>et al.</i> (2019)	<i>Scomber scombrus</i>	100%, 70%, 50%, 40% O ₂	10 min; acute	No effect on NND or orientation	–
		Cook <i>et al.</i> (2014)	<i>Embiotoca lateralis</i>	100%, 15–75% measured at 5% intervals	5 h; acute	No effect on NND or polarity	–
		Domenici <i>et al.</i> (2002)	<i>Clupea harengus</i>	15–95% O ₂ , measured at 5% intervals	4 h; acute	Increased school length, width, and depth at 20–25% O ₂	–
		Hayes <i>et al.</i> (2019)	<i>Luciobarbus bocagei</i>	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)	<i>Carassius auratus</i>	~88%, 11% O ₂	5.5 h; acute	Increased school depth, no effect on school width or length	– reported
		Moss & Mcfarland (1970)	<i>Engraulis mordax</i>	89%, 7.6%, 6.9% O ₂	2 h; acute	Increased MDSCS and reduced polarity at low O ₂	–
		Pineda <i>et al.</i> (2020)	<i>Corydoras aeneus</i>	100%, 60%, 30% O ₂	4 h; acute	No effect on IID	0
Acidification	Sociability	Kleinhappel <i>et al.</i> (2019)	<i>Gasterosteus aculeatus</i>	pH 6.25, 6.3, 8.4	2 days; acute	No effect on time spent associating with a conspecific	+
		Maulvault <i>et al.</i> (2018)	<i>Argyrosomus regius</i>	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 <i>et al.</i> (2016)	<i>Pangasianodon hypophthalmus</i>	pH 7.2, 5.8	7 days; acclimated	No effect on time near conspecifics	–
	Group cohesion	Cattano <i>et al.</i> (2019)	<i>Chromis viridis</i>	pH 7.9, 8.1	5 days; acute	No effect on IID	–
		Duteil <i>et al.</i> (2016)	<i>Dicentrarchus labrax</i>	pH 7.82, 8.03	59 days; acclimated	No effect on number of nearest neighbours or IID	No effect reported
		Kwan <i>et al.</i> (2017)	<i>Chromis punctipinnis</i>	pH 7.7, 7.9, increasing and fluctuating pH	11 days; acclimated	No effect on IID	+
		Lopes <i>et al.</i> (2016)	<i>Atherina presbyter</i>	pH 7.6, 8.1	7, 21 days; developmental	Increased NND and CEI following 7 days exposure; reduced NND following 21 days exposure	–
		Mitchell <i>et al.</i> (2022)	<i>Abudefduf vaigiensis</i> ,	pH 7, 8.1	6 days; acute	Increased IID in mixed-species pairs. No effect on amplitude variability or oscillation frequency	–

			<i>Atypichthys strigatus</i>				
		Moss & Mcfarland (1970)	<i>Engraulis mordax</i>	pH 6, 6.1, 7.75	90 min; acute	Increased MDCS and reduced polarity at low pH	–
		Ross <i>et al.</i> (2001)	<i>Rhinichthys atratulus</i>	pH 6.6, 6.8	1 day; acute	No effect on number of contacts between conspecifics	0
Combined stressors	Sociability	Maulvault <i>et al.</i> (2018)	<i>Argyrosomus regius</i>	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 <i>et al.</i> (2022)	<i>Abudefduf vaigiensis</i> , <i>Atypichthys strigatus</i>	23 °C + pH 8.1, 26 °C + pH 8.1 pH 7, 8.1, combinations	6 days; acute	No effect on group cohesion	–
		Pineda <i>et al.</i> (2020)	<i>Corydoras aeneus</i>	30 °C + 60%, 30 °C + 30% O ₂	Temperature 14 days; acclimated + hypoxia 4 h; acute	No effect on IID	0

CEI, Clark-Evans Index; IID, inter-individual distance; MDCS, mean distance from centre of shoal; NND, nearest-neighbour distance.

2.4.2. 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 2.3). Temperature change from control levels ranged from $<+1$ to $+20$ °C (Figure 2.6A). 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 2.3).

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 2.3). 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 2.4).

Table 2.4. 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	<i>p</i> MCMC
Intercept	0.494	-1.960	1.793	1655	0.995
Temperature change (<i>versus</i> 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

2.4.3. 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 2.3). One additional study investigated effects on individual sociability, for which we found no significant effect (Table 2.3). Reduction in oxygen level for hypoxia treatments ranged from <1% to >95% (Figure 2.6B). 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 (Figure 2.7A). The correlation between oxygen availability and effect on sociability was non-significant (Table 2.5). 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 (Figure 2.7B), 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.

Table 2.5. 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	<i>p</i> MCMC
Intercept	560.5	−44854	57484	1800	0.846
Change in oxygen availability (<i>versus</i> 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

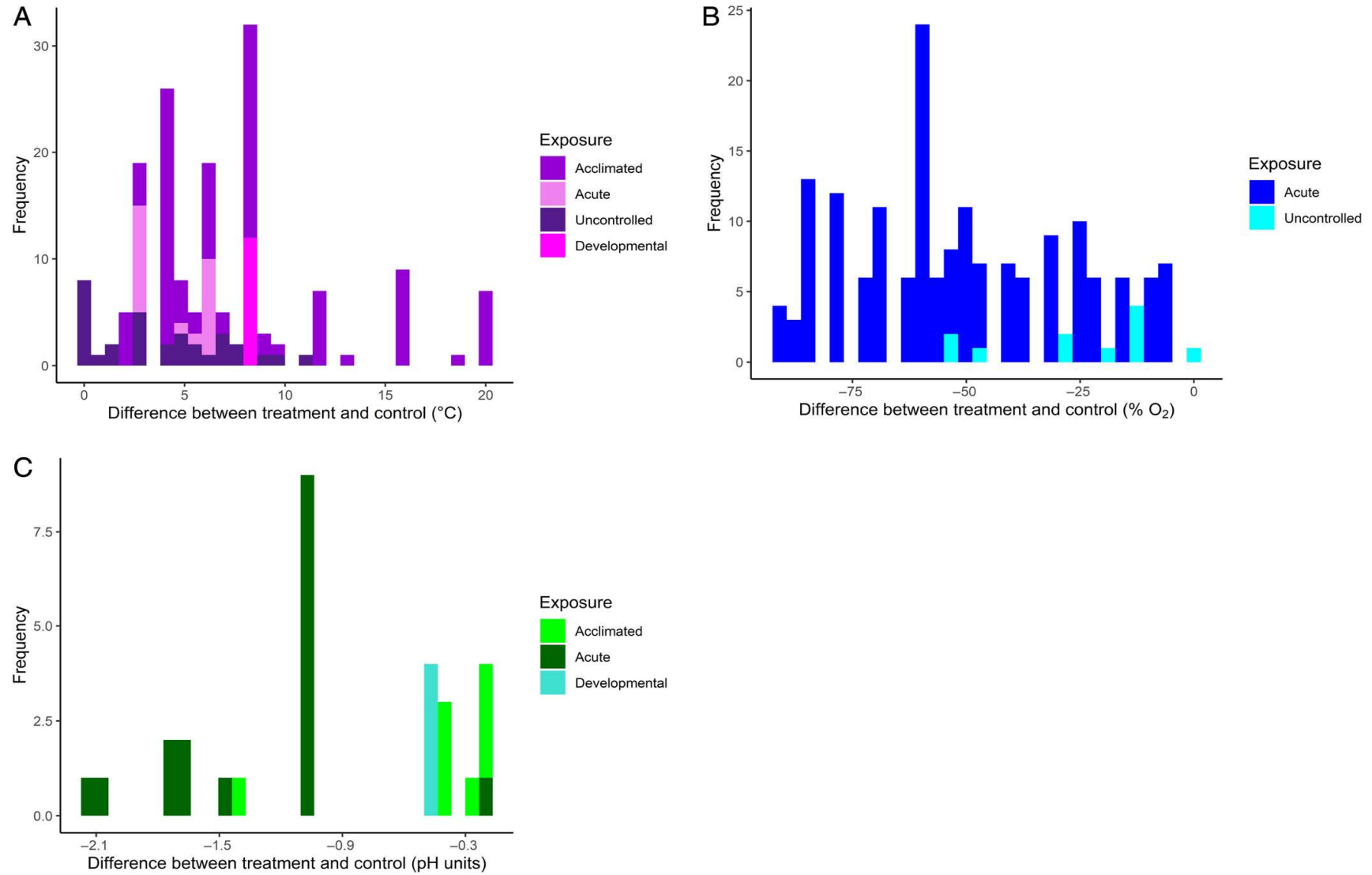


Figure 2.6. Frequency histograms of trials of sociability or group cohesion according to degree of change in A. temperature, B. oxygen concentration and C. pH (acidification).

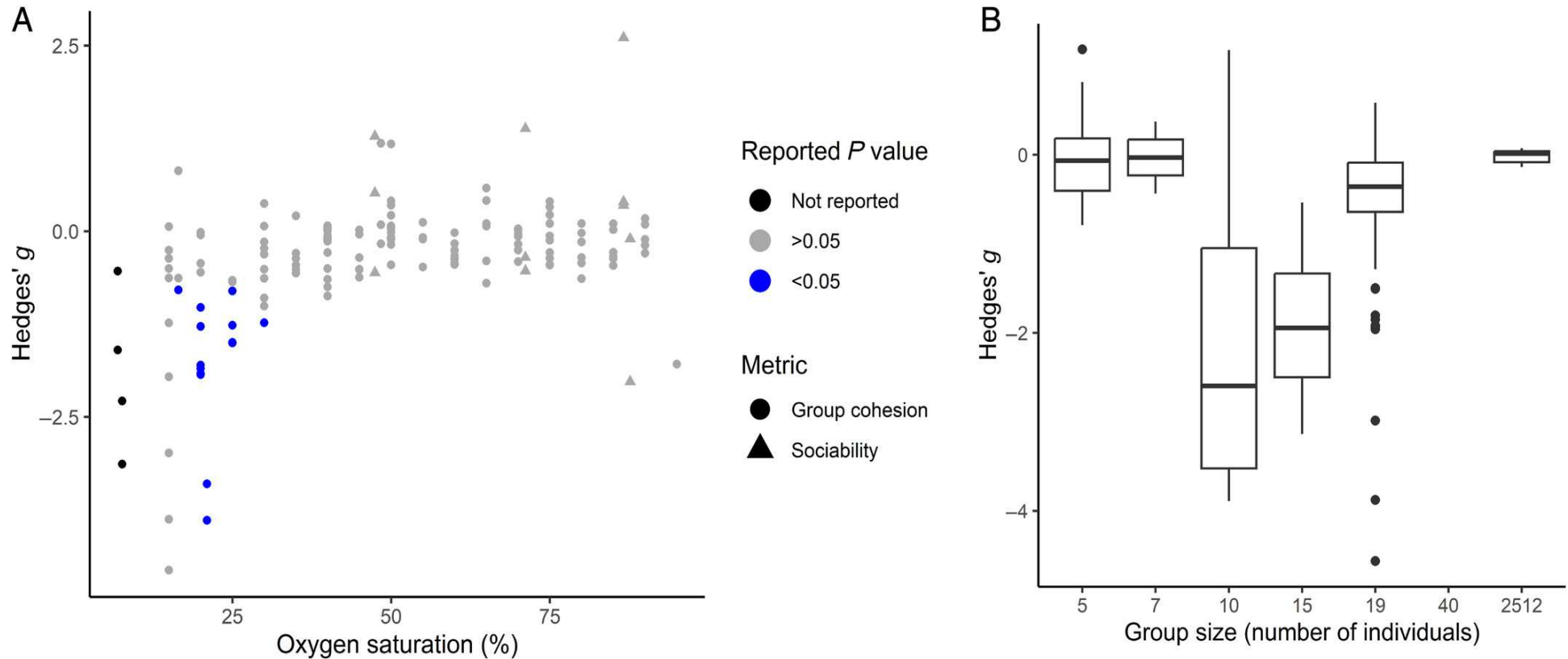


Figure 2.7A. Effect size (Hedges' g) of hypoxia on group cohesion and sociability in fishes. Reported p values from the original studies are also indicated. **B.** Effect of group size on mean effect sizes for changes in group cohesion in response to hypoxia in fishes. Black lines show the median, boxes 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.

2.4.4. Acidification

Seven studies investigated the effects of acidification on group cohesion, for four of which we found negative effects 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 2.3). 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 2.3). Changes in pH during treatments ranged from -0.21 to -2.15 pH units (Figure 2.6C). 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 2.6). 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; A. Mitchell et al., 2022; Moss & McFarland, 1970).

Table 2.6. 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 (<i>versus</i> 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

2.4.5. 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 2.3), one on sociability (Maulvault et al., 2018) and one on cohesion (A. Mitchell et al., 2022).

2.5. 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 (Nati et al., 2018; Pilakouta et al., 2020) 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 observed in this review may be explained, and suggest directions in which much-needed further research may proceed.

2.5.1. Temperature

As increasing temperature leads to an elevation in metabolic rate and spontaneous activity level in many fish species (Colchen et al., 2016; Davis et al., 2019), 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 (Conrad et al., 2011; Killen, Fu, et al., 2016). 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; A. 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 (Figure 2.6A). Fish may be more likely to respond to acute thermal effects, showing exaggerated immediate changes in metabolism, aerobic scope and blood glucose levels (Johansen 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 (Johansen et al., 2021). As metabolic factors have been found to affect social behaviour (Killen, Fu, 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. (2023) 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., 2023). 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 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., 2016; 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 et al., 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, Cortese, 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, Marras, 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).

2.5.2. 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 (Domenici et al., 2017; Lefrançois et al., 2009). 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 (Domenici et al., 2007; Lucon-Xiccato et al., 2014; Nilsson et al., 1993; Schellart & Wubbels, 1998). 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 (Figure 2.7A). 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 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 (Figure 2.7B). 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 (Domenici et al., 2017; Moss & McFarland, 1970). 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 (Figure 2.6B). 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.

2.5.3. 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 (Ishimatsu et al., 2004; Kwong et al., 2014). 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 2.3). 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., 2017). 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., 2017).

2.5.4. 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 (A. 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 et al., 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 (R. 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.

2.6. Functional Implications

Direct benefits of shoaling and schooling in fishes include protection from predators and swimming energetics. Being 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 (A. Ward & Webster, 2016c). 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 et al., 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 (Lefrançois et al., 2005; Lefrançois & Domenici, 2006). 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 (Breitburg et al., 1994; Shoji et al., 2005), 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 (L. 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).

2.7. 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 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.

Chapter 3

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

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3.1. 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 meta-analysis 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.

3.2. 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 & 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, Cortese, 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, Gore, et al., 2022).

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, 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 17 α -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, Martin, et al., 2022b; Fenske et al., 2020; Kidd et al., 2007).

Inorganic chemical pollutants like metals cannot be biologically transformed, and are often acutely toxic, with the potential for endocrine disruption after chronic exposure (Shahjahan et al., 2022; Vieira et al., 2009). 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 & Pottinger, 1989; Simpson et al., 2016), they have also been found to affect various forms of behaviour (Mickle & Higgs, 2018; Neo, Parie, et al., 2015; Neo, Ufkes, et

al., 2015; 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 & Pitcher, 1980). If metabolic needs increase due to pollutant exposure, individuals may become less sociable to prioritise foraging and reduce competition (Killen, Fu, 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, Cortese, 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 meta-analysis 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 & Pauly, 2023), and may thus be exposed to almost every aquatic environmental pollutant.

3.3. Methods

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

3.3.1. Literature searches

Searches of the literature were carried out from October to December 2022 (Figure 3.1). 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.

3.3.2. 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 3.1).
- (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.

Web of Science, Scopus, ProceedingsFirst, Google Scholar databases

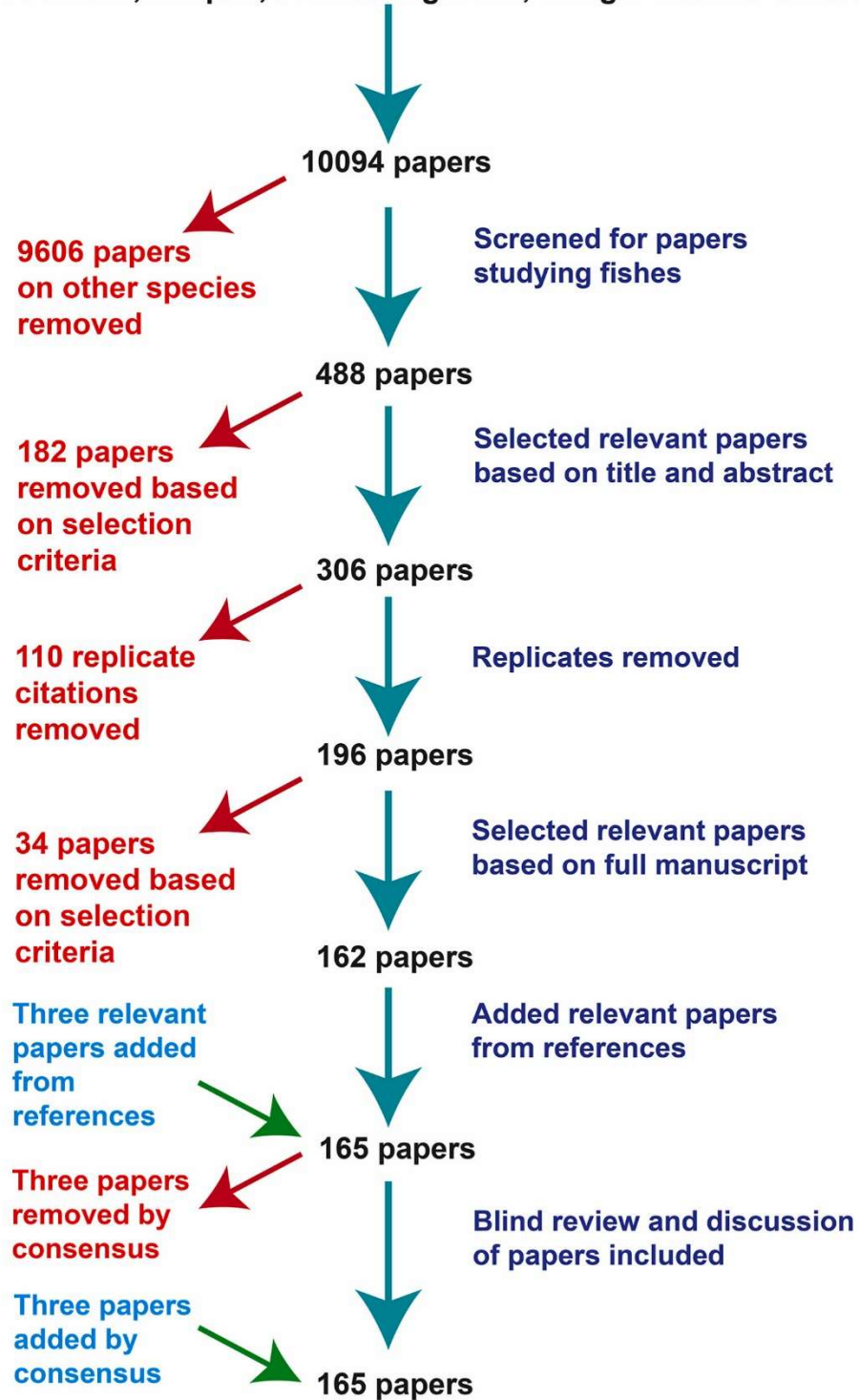


Figure 3.1. Flow diagram illustrating paper selection process for systematic review.

- (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).

Table 3.1. 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	

3.3.3. Statistical analysis

Meta-analysis 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 & 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.

3.4. Results

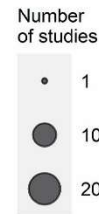
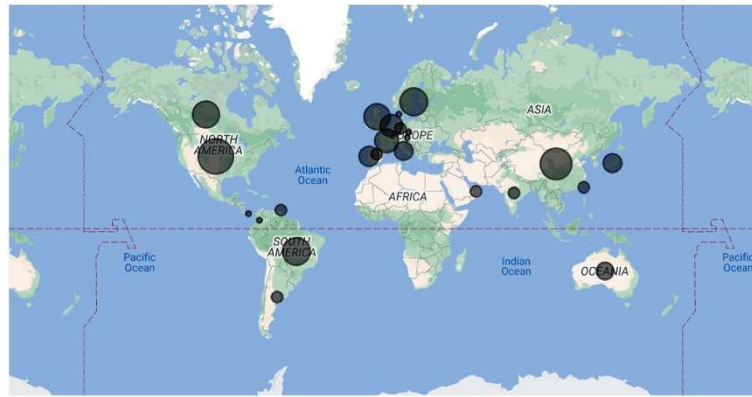
3.4.1. Literature overview

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 3.1; Figure 3.1). Of these, 162 were found from literature searches, while a further three were identified from reference sections of papers (Figure 3.1). 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 (Figure 3.2A), a significant geographical bias was present, with 66% of studies being carried out in North American and European countries.

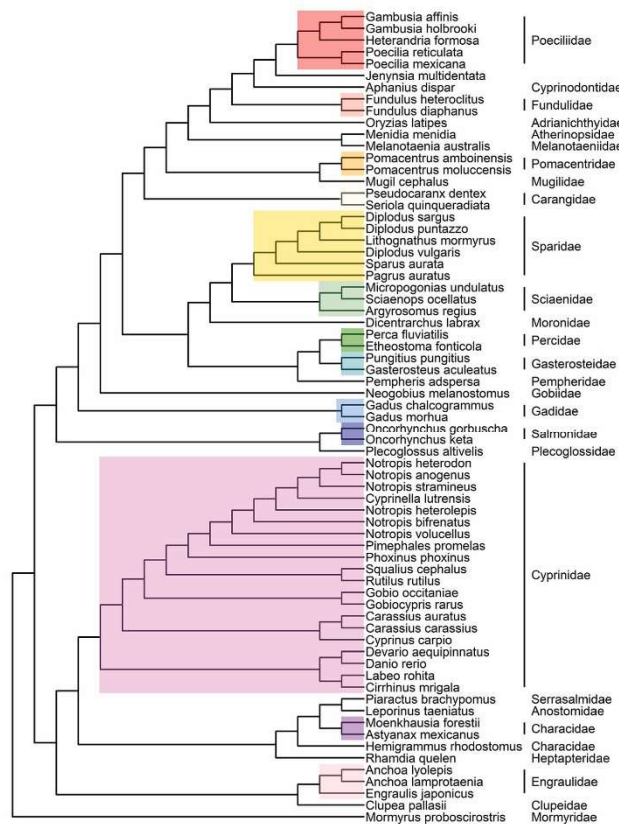
The effects of chemical and non-chemical pollutants on fish social behaviour were studied in 69 species (Figure 3.2B). Of these, 20 were in the family Cyprinidae, with the most-commonly used species being the zebrafish *Danio rerio* ($n = 43$). Phylogenetic diversity of species used across studies was 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 ($\lambda = 6.71 \times 10^{-5}$, $p = 1$).

Results of all studies for which effect size could be calculated ($n = 141$) are summarised in Figure 3.3. 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.

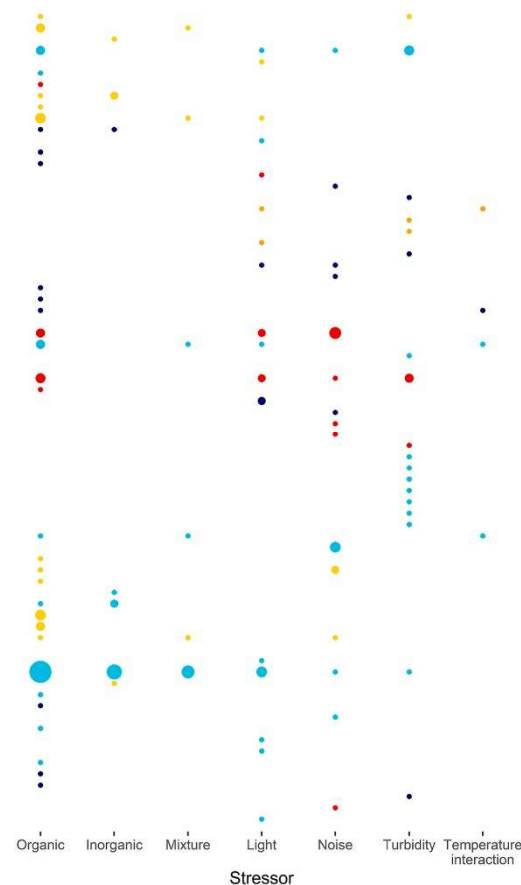
Figure 3.2A. Map showing locations of studies on the effects of pollution on sociability and/or group cohesion in fish species. Larger circles indicate more studies. B. Phylogenetic tree showing species used in studies of the effects of pollutants on fish behaviour. Family to which each species belongs 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.



A



B



3.4.2. 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 3.1; Figure 3.3). Of studies of mixtures, 31% ($n = 5$) studied mixtures of organic and inorganic pollutants. 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 3.2).

Table 3.2. 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

	Sociability	No effect	3
		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

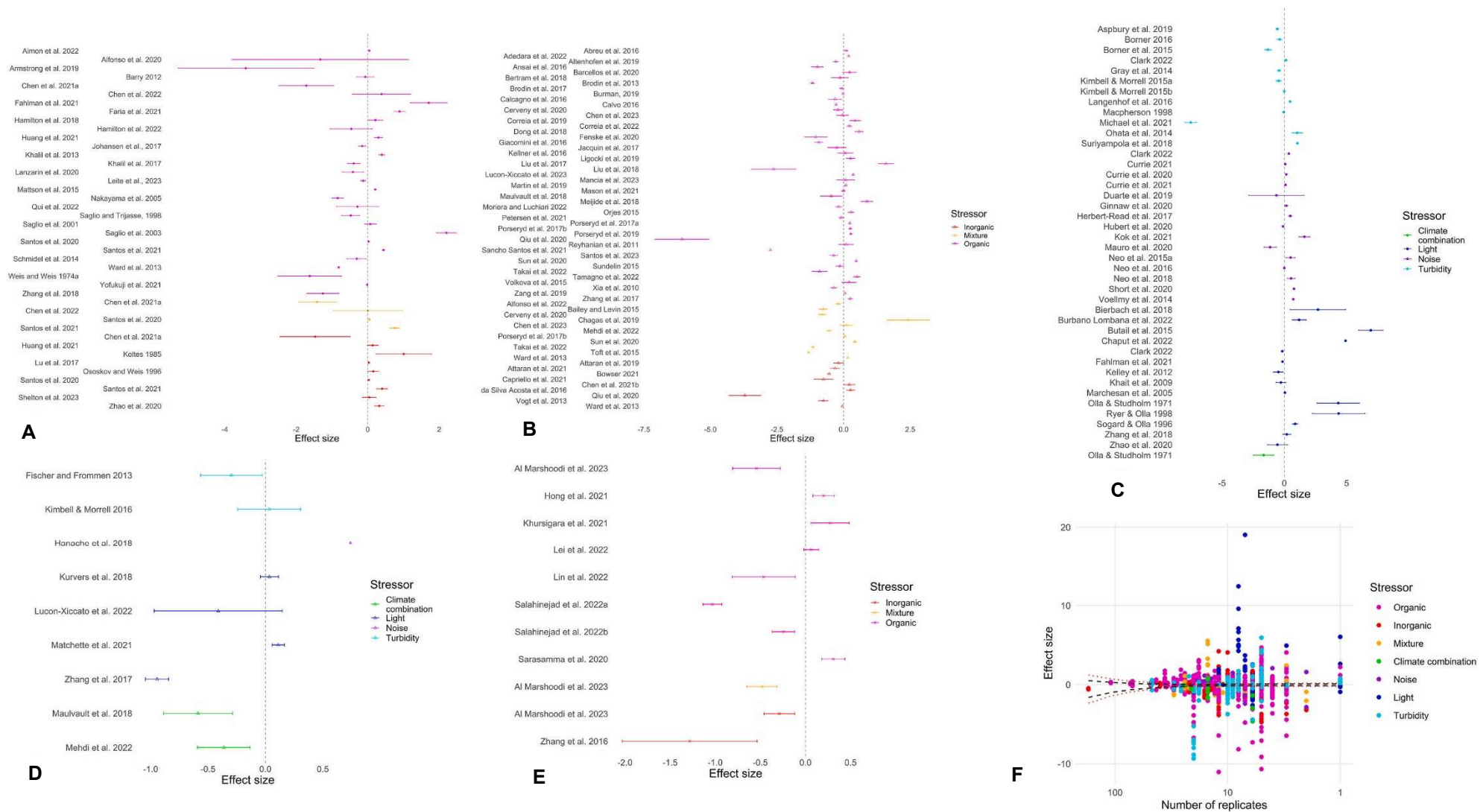


Figure 3.3. Forest plots showing mean and standard error of effect sizes calculated for each study included in meta-analysis. **A.** studies of effects of chemical pollutants on group cohesion; **B.** studies of effects of chemical pollutants on sociability; **C.** studies of effects of non-chemical 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 meta-analysis. Black dashed lines indicate 95% confidence interval; red dashed lines indicate 99% confidence interval.

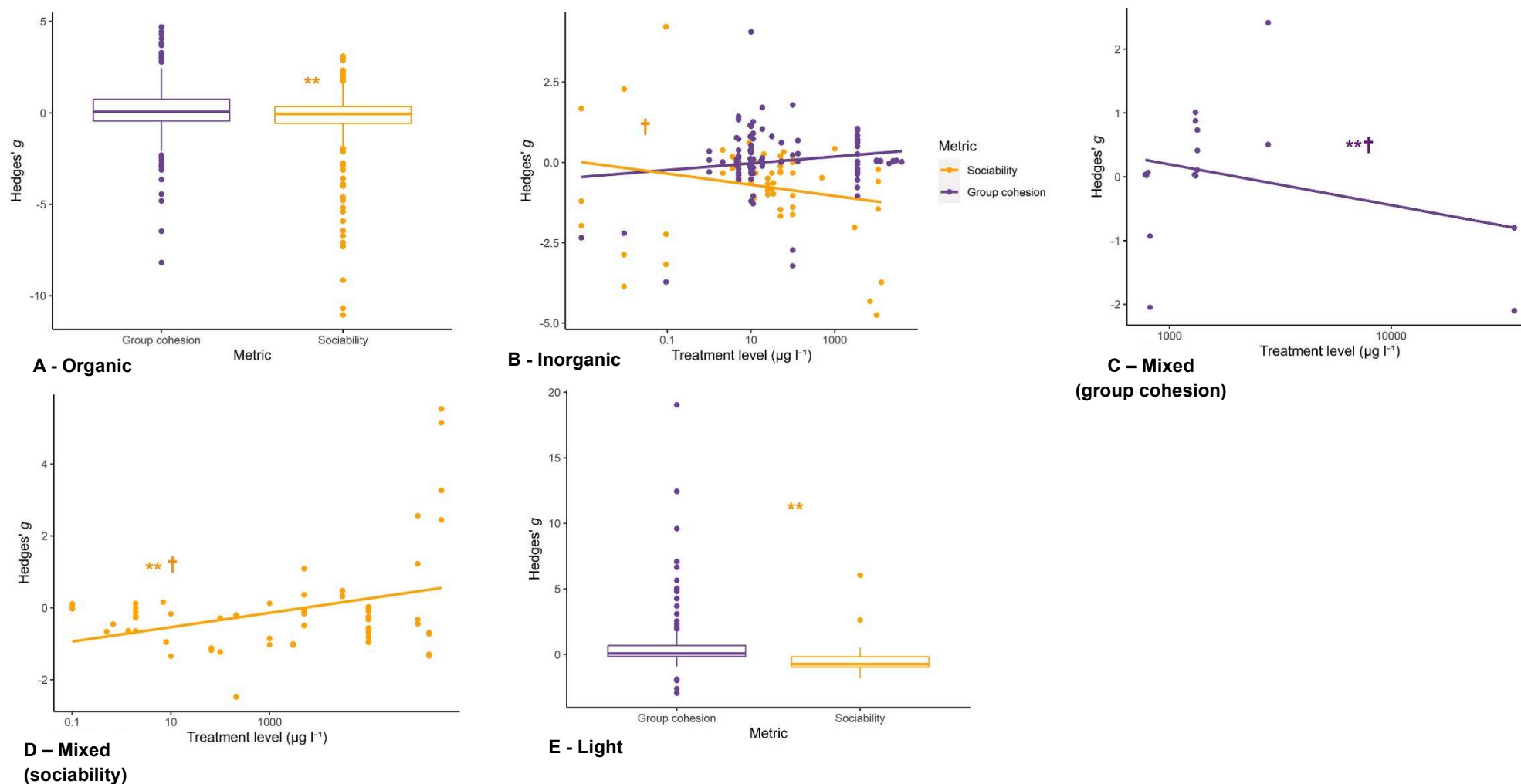


Figure 3.4. Effect on sociability and group cohesion in fish species according to level of **A.** organic chemical pollutants, **B.** inorganic chemical pollutants, **C.** mixed chemical pollutants (group cohesion), **D.** mixed chemical pollutants (sociability) and **E.** light. Group cohesion and sociability are plotted separately in the case of mixed chemical pollutants due to the need to use a logarithmic scale for the sociability plot (x 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 $p < 0.001$.

Meta-analysis 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 3.2; Supplementary Table 3.3; Figure 3.4A; Figure 3.4B). In the case of inorganic pollutants, however, this was dependent on pollutant concentration, with greater reductions in sociability at higher concentrations ($PM = -1.453$, $p < 0.001$) (Figure 3.4B). 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 ($PM = -1.663$, $p < 0.01$) (Figure 3.5A).

For mixtures of chemical pollutants, meta-analysis 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 (Figure 3.4C). 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 3.4; Figure 3.4D). 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 (Figure 3.5B). The reduction in cohesion following exposure was found to be magnified in larger groups ($PM = -0.242$, $p < 0.01$) (Supplementary Figure 3.1).

3.4.3. *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 3.1; Table 3.2; Figure 3.3).

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 3.5; Figure 3.5C). In addition, cohesion was significantly greater

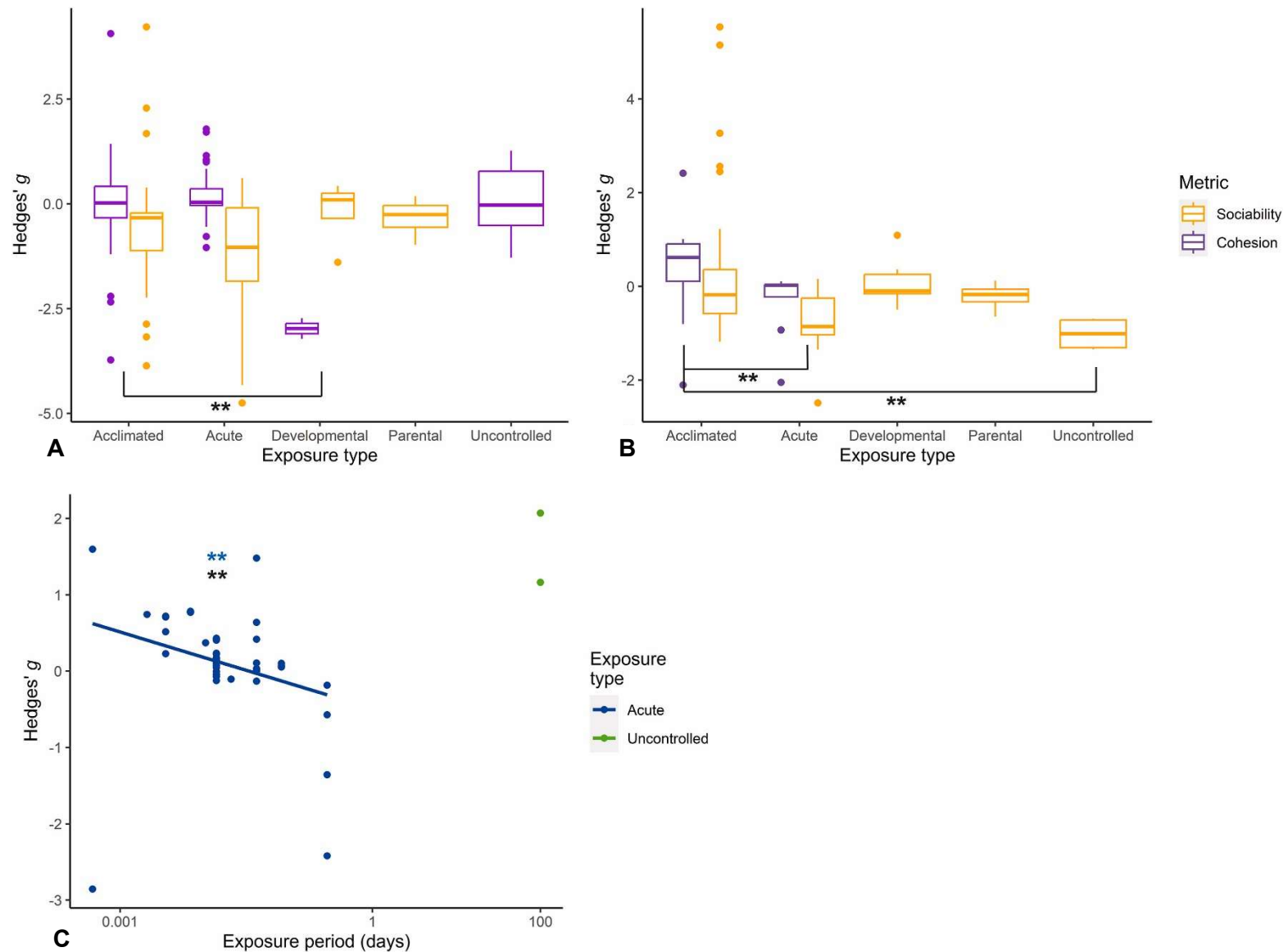


Figure 3.5. Effect of A. inorganic chemical pollutant exposure, B. mixed chemical pollutant exposure and C. noise on fish group cohesion and sociability according to exposure type and period. Acclimated = >7d exposure; acute = <7d exposure; developmental = exposure during egg or larval stage; parental = 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 $p < 0.001$.**

following uncontrolled exposure compared with acute exposures ($PM = 406.0, p < 0.01$). Meta-analysis 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 3.6, Supplementary Table 3.7). Individual sociability, however, was reduced in fish exposed to increased light levels ($PM = -3.038, p < 0.01$) (Supplementary Table 3.6; Figure 3.4E).

3.5. 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, Gore, et al., 2022; 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 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.

3.5.1. *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 behavioural response to a specific contaminant can be challenging under varying exposure conditions (Wong & 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, Marras, 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 (V. C. Renick et al., 2016). Changes to swimming speed may lead to disruption of group cohesion or fragmentation of shoals (Killen, Marras, et al., 2017). Overall, the mechanistic understanding of behaviours caused by chemical pollutants, especially sociability, remains complex and expansive (Pyle & Ford, 2017).

While we found evidence for reduced sociability (Figure 3.4A; Figure 3.4B), 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 meta-analysis 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 (Figure 3.4C),

though these mixtures also appeared to produce an increase in sociability (Figure 3.4D). This may indicate masking of, or variance in, the individual response in groups (Bertram, Gore, et al., 2022; 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 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 Figure 3.1). 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., 2004; 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 meta-analysis 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 (Figure 3.4B), 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 & Wood, 2011; Birceanu et al., 2008; Rogers & 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 & 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 & 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 & 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 (Figure 3.5A), suggesting greater vulnerability at the embryonic or larval stages. However, as only two studies of developmental exposure have been carried out (Chen, Lei, et al., 2021; Chen, Li, et al., 2021), 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 meta-analysis 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 (Figure 3.5B). 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.

3.5.2. *Non-chemical pollutants*

No effects of turbidity were found by our meta-analysis 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 meta-analysis to reduce sociability while having no effect on cohesion (Figure 3.4E). 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.

Meta-analysis 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 & 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 meta-analysis. 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, Parie, et al., 2015; Neo, Ufkes, et al., 2015), an effect that was also found by our meta-analysis (Figure 3.5B). 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, Ufkes, et al., 2015). 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 & 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 3.2). 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 meta-analysis found a greater increase in cohesion following uncontrolled compared with acute exposure (Figure 3.5C), 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 (Brüning 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.

3.6. 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 & 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.

Chapter 4

Changes to group dynamics reflect changes in individual behaviour under thermal stress in a model fish species

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4.1. Abstract

As global temperatures rise, the ways in which organisms respond and the wider implications of these responses at the level of social groups are of increasing interest. Temperature can affect individual and group level social behaviour in fish species, and individual behavioural traits can affect group dynamics. However, it is still unknown whether the links between group dynamics and traits of individuals within a group may be affected by temperature. Here, we investigated whether effects of temperature on individual-level behaviour would be reflected in changes in group level behaviour in rummy-nose tetras, *Hemigrammus rhodostomus*, using tracking of individuals with quantified individual behavioural traits. We further tested whether measures of individual risk-taking behaviour, sociability, and activity level would impact position or interactions of these same individuals within groups at 24°C, 27°C, and 30°C. Less-social, less-active individuals that displayed greater risk-taking behaviour were more likely to swim at the front of a shoal, indicating that these individuals may have a greater influence on group decision making. In general, speed and polarisation at the group and individual levels increased with temperature. However, swimming speed showed a decline with temperature in social, less-active fish and groups containing these, while group polarisation was

reduced at high temperatures in groups containing larger fish. Our results indicate that behavioural traits and body size of individuals affect the role of those individuals within groups and group-level behaviours, but that these relationships are also modulated by environmental factors. These findings demonstrate the importance of incorporating abiotic factors when linking individual and group behaviour - a key consideration for species in changeable environments.

4.2. Introduction

The effects of rising temperatures resulting from anthropogenic activities on organisms and ecosystems are of critical research interest. Plastic responses or evolutionary adaptation to changing conditions are key to understanding the scope for organisms to survive and maintain their ecological functions (Wong & Candolin, 2024). While such coping mechanisms may occur at the individual level, many animals live in groups and their behavioural responses are shaped by social interactions. Studying how individual-level adaptation translates to changes at higher levels of organisation is therefore vital for a thorough comprehension of ecological resilience, given that processes at the level of the social group (Ioannou, 2017) or population (Fronhofer et al., 2015) can feedback to impact individual fitness.

Animal behaviours are modulated through a range of drivers and are often affected by energy needs (Seebacher & Krause, 2017). In endotherms, changes in the energy landscape can lead to changes in social structure. In weaver birds *Philetairus socius*, for example, social behaviour may be reduced at higher temperatures as individuals prioritise thermoregulation (Rat et al., 2020). Within aquatic systems, the effects of temperature on animal behaviour may be especially prominent. Many aquatic organisms are ectothermic and so their body temperature relies on that of the external environment. As temperatures increase, metabolic rates in ectotherms tend to increase (Clarke & Johnston, 1999; Nati et al., 2018; Pilakouta et al., 2020), often leading to increased food demand, activity, changes to energy budgeting, and knock-on effects on behaviours such as foraging (Garrido et al., 2016). While group foraging often leads to improved food-finding potential (Pitcher et al., 1982), food resources are also shared and competed for among group members (Killen, Cortese, et al., 2021). Individuals with higher metabolic needs or those that are less able to compete may therefore be more likely to leave a group at higher temperatures to avoid sharing food resources, leading to reduced tendency to be social (sociability) (Ioannou, 2017; Killen, Cortese, et al., 2021). Increased foraging frequency (Garrido et al., 2016) and

activity at higher temperatures (Bartolini et al., 2015) may also make fish less risk-averse (McKenzie et al., 2015; Metcalfe et al., 2016), leading to increased risk-taking behaviour (Ioannou, 2017; Killen, Fu, et al., 2016). While individuals of some ectothermic species show reduced individual sociability at higher temperatures (e.g. zebrafish *Danio rerio* (Angiulli et al., 2020) and stickleback *Gasterosteus aculeatus* (Cooper et al., 2018; Pilakouta et al., 2023)), others show no effect (Mehdi et al., 2022; Monnet et al., 2023; Tang & Fu, 2021; Tiddy, Munson, et al., 2024; Weetman et al., 1999) or an increase in sociability with warming (Maulvault et al., 2018). In natural systems, behavioural response to temperature may also be modulated by other abiotic (Maulvault et al., 2018) or biotic stressors (Weetman et al., 1999). How abiotic factors such as temperature modulate behaviour is a key element in understanding intraspecific interactions, particularly in gregarious species (Tiddy, Munson, et al., 2024).

Just as individual behavioural responses are modulated by different drivers, behavioural dynamics and responses to stressors at the group level are dependent on the responses of individuals within the group (Jolles, King, et al., 2020; Killen, Cortese, et al., 2021). In gregarious species, the behavioural and physiological traits of individuals can help to determine the role and interactions of these individuals within a group, which in turn will influence group-level behaviours such as group speed and polarisation (Brown & Irving, 2014; Herbert-Read et al., 2013; Jolles et al., 2017; Killen, Marras, et al., 2017). For example, Jolles et al. (2017) found that individuals often found at the front of the shoal in group trials of stickleback *Gasterosteus aculeatus* were more active and less social in individual settings. Fish with a greater tendency to risk-taking behaviour have also been found to be more likely to lead a shoal or initiate movements (Bevan et al., 2018; Harcourt et al., 2009; Nakayama et al., 2012). Individuals at the front of the group tend to influence group decisions (N. Miller et al., 2013; Nakayama et al., 2012), potentially affecting group foraging behaviour, predation risk, and other interactions with hetero- or conspecifics (Jolles, King, et al., 2020; Killen, Cortese, et al., 2021). In addition, behavioural traits and thus group dynamics may be influenced by morphological factors such as body size (Johansen et al., 2014; Jolles, King, et al., 2020; Romenskyy et al., 2017). Understanding how changes to behaviour at the individual level may correspond to changes in dynamics within groups or populations is therefore key to understanding the ecological relevance of individual-level behavioural changes (Domenici et al., 2017; Jolles, King, et al., 2020; Tiddy, Munson, et al., 2024).

In the context of abiotic stressors, an emerging challenge is to understand whether behavioural effects observed in individuals translate into changes in group dynamics (Luo et al., 2024). As with individual sociability, the effects of temperature on cohesive, polarised schools in fishes are mixed (e.g., (Davis et al., 2019; Fahlman et al., 2021; Kuruvilla et al., 2023; Mukherjee & Bhat, 2024), reviewed in Tiddy et al., 2024), and can be altered by additional stressors such as pH (A. Mitchell et al., 2022), turbidity (Zanghi et al., 2023), and predation threats (Kuruvilla et al., 2023). Although abiotic stressors may alter schooling through their effects on individual behaviour (Luo et al., 2024), we still know relatively little about how variation among individuals maps onto their roles within groups. This is complicated by the fact that the social environment is itself a strong determinant of individual behaviour (Killen et al., 2026; Tiddy et al., 2025; Webster et al., 2007; Webster & Ward, 2011) and may interact with abiotic conditions (Kuruvilla et al., 2023). Examining behaviour across different social contexts may therefore help reveal how individual responses to temperature and other stressors scale up to influence group structure and dynamics (Jolles et al., 2017; Magnhagen & Bunnefeld, 2009; Tiddy et al., 2025; Webster & Ward, 2011).

As ectotherms, and as animals that display social behaviour at one or more life stages, fishes are ideal study taxa for investigating effects of acute thermal stress on social behaviour. Although previous studies show that temperature can influence both individual sociability and group-level shoaling behaviour, we still know little about whether temperature changes how individuals with different behavioural tendencies contribute to group dynamics. In other words, it remains unclear how thermal stress modifies the links between individual behavioural traits and the roles individuals play within shoals. In the present study, we examined how acute thermal stress affects relationships between individual behavioural traits (activity, risk-taking, and sociability) and individual and group-level shoaling dynamics. We expected behavioural responses to temperature measured in isolated individuals to be reflected in their behaviour in groups and, in turn, in emergent changes in shoal dynamics. We used the rummy-nose tetra *Hemigrammus rhodostomus* (Calovi et al., 2018; Lafoux et al., 2024; Lei et al., 2020; Wood et al., 2014), a schooling tropical freshwater fish (Killen et al., 2026), which does not display aggressive or territorial behaviour and therefore is well suited for studies of social behaviour.

4.3. Methods

4.3.1. Experimental overview

To examine how acute temperature exposure influenced behaviour across both solitary and social contexts, the same individually tagged *H. rhodostomus* were tested in a series of individual and group behavioural assays (Figure 4.1). Fish were first assessed individually for risk-taking behaviour, measured here as tendency to leave a shelter (mean distance to a shelter) and sociability, after which group behaviour was tested using the same individuals in their original social groups. During trials, treatment fish were exposed acutely to each of three temperatures (24°C, 27°C, and 30°C), representing ecologically relevant thermal conditions for the species. All individuals and groups experienced all three temperatures over the course of the experiment. Temporal control trials conducted entirely at 24°C were used to account for potential effects of repeated handling, acclimation, and time spent in the arena. This repeated-measures design allowed us to determine whether behavioural traits measured in isolated individuals predicted the interactions of those same individuals within groups and their influence group dynamics under different thermal conditions.

4.3.2. Study animals

Wild-caught *H. rhodostomus* were acquired from a reputable trader and arrived on 16/10/2023. Fish were initially housed in two large (280 l) tanks containing ~50 individuals per tank, where they were allowed one week to acclimate and recover from transit. Following this, fish were moved into smaller (10 l) tanks in groups of six individuals. Eight groups of six were designated as treatment groups. A further four groups of six were designated as control groups, however the individuals in one of these groups had to be used to replace individuals in other groups, including one treatment group (TG3), due to mortality, resulting in three control groups. The remaining four groups of six were used as stimulus fish in sociability trials. Following placement in groups of six, individuals in control and treatment groups were uniquely tagged using elastomer tags (Northwest Marine Technology Inc.) to allow individuals to be identified. Individuals were

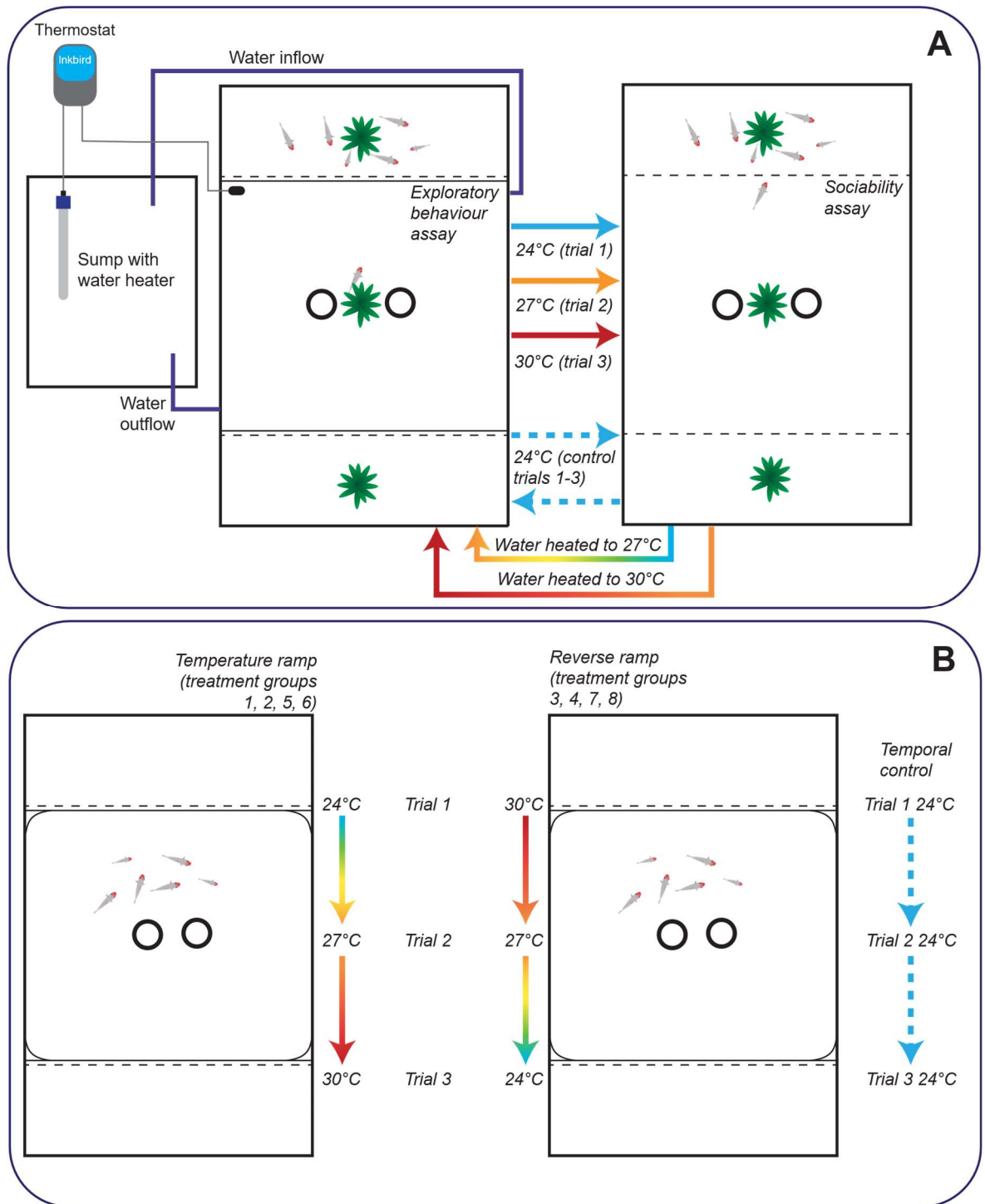


Figure 4.1. Schematic showing arena setup and temperature ramping procedures for **A)** individual behaviour trials and **B)** group behaviour trials. In individual behaviour trials, opaque inserts (thin black lines) were removed between risk-taking behaviour and sociability trials, to allow fish to see the stimulus shoal. Focal fish remained in the arena. Inserts were then replaced prior to water being heated for the next risk-taking behaviour trial. Fish were separated from the stimulus shoal by transparent perspex sealed with aquarium-safe silicone (dashed black lines). The temperature regulation setup was the same for all trials but is only illustrated once for simplicity. Solid arrows refer to procedures carried out in temperature ramp trials ($n = 8$ groups, $n = 48$ individuals), dashed arrows refer to procedures carried out in temporal control trials ($n = 5$ groups, $n = 46$ individuals).

anaesthetised for tagging and measuring of standard length (mm) and mass (g) using benzocaine solution (2.5 mg l^{-1}). All treatment groups and individuals were used in behavioural trials at three temperatures (24°C , 27°C , 30°C), representing close to the full range of temperatures experienced by *H. rhodostomus* in the wild (Beltrão dos Anjos et al., 2017; Fróis et al., 2021). Control groups were used in three successive trials at 24°C to test for temporal changes over trials within the same group. All groups were held at 24°C and a dissolved oxygen concentration of 100% air saturation. Pilot trials were carried out on three groups (TG2, 3, 4) and individuals from these groups to check response of fish to the arena and ensure that fish would resume normal behaviour following handling. Pilot trials were carried out a minimum of 5 days prior to the same fish being used in treatment trials.

4.3.3. *Experimental setup*

A visualisation of our experimental setup is shown in Figure 4.1. Two large opaque plastic tubs, lined with white paper to improve contrast of the fish and provide a uniform environment, were divided into two areas creating four behavioural arenas. These arenas were then divided into three parts, with a smaller chamber ($11.5 \times 36.5 \text{ cm}$) at each end and a larger, central chamber ($32.8 \times 36.5 \text{ cm}$), separated by transparent PVC dividers. These dividers were sealed with aquarium-safe silicon to prevent water exchange between chambers. Opaque removable inserts were cut from white PVC plastic; these could be placed next to the transparent dividers to hide the end chambers from the central chamber. All chambers were filled with water to a depth of 6 cm (volume 12.2 l). Each arena contained a water inlet and outlet, which were connected to a sump (one sump per arena; sump volume 20 l; total volume per arena 32.2 l) via two Eheim 10 l min^{-1} pumps. Sumps each contained a heater. The heating pipe was connected to an Inkbird thermostat, the sensor of which was placed in the central chamber to ensure that the temperature within the central chamber would be regulated via the sump. This allowed the temperature within the central chamber to be regulated to within $\pm 0.3^{\circ}\text{C}$, with occasional fluctuations of $\pm 1^{\circ}\text{C}$ due to the high volume of water. As it was found in pilot trials that tetra fail to resume normal behaviour when not provided with any form of enrichment, enrichment was provided in the form of an artificial plant placed in the centre of the central chamber. In addition, two upright opaque pipes were placed either side of the plant. Additional artificial plants were also placed in the smaller chambers at each end of the arena, to provide shelter to stimulus fish (Figure 4.1).

4.3.4. *Individual behavioural trials*

Sociability and risk-taking behaviour were assessed in all individuals from treatment and control groups to examine whether temperature-induced differences in behavioural traits measured in individual assay contexts would influence behaviour when fish were subsequently placed in a shoal. Shoals of six stimulus individuals were placed in one of the side chambers in each arena (Figure 4.1). The side on which stimulus fish were placed initially was determined randomly, after which the side in which stimulus fish were placed was alternated after every trial. During risk-taking behaviour trials, the opaque inserts were left in, meaning that the focal individual placed in the central chamber could not see the conspecifics in the adjacent chamber. As dividers were sealed, fish were not alerted to the presence of the conspecific shoal by olfactory cues. Focal individuals were taken from treatment or control groups and placed in the central chamber. Fish were allowed 30 minutes of free swimming to settle and resume normal behaviour, i.e., normal opercular rhythm and swimming behaviour rather than freezing or darting around the tank due to stress. Fish were then filmed from above using a GoPro Hero 6 Black in linear mode with a frame rate of 25 fps and 1080p resolution for ten minutes, to assess risk-taking behaviour. Videos were processed using the behavioural tracking software EthoVision (Noldus et al., 2001). Median speed of movement during the trial (cm s^{-1}), thigmotactic behaviour (percentage time spent near the chamber wall) and mean distance to the nearest shelter (plant and pipes; cm) were recorded based on x-y coordinates in each frame.

Following the end of risk-taking behaviour trials, focal individuals remained in the arena, the camera was switched off, and both opaque panels were removed to allow the test fish to see the stimulus conspecifics in one of the end chambers. Fish were allowed five minutes to recover from the disturbance caused by removing the opaque panels, following which they were again filmed from above for ten minutes, to assess sociability. Mean distance to the stimulus shoal (cm) and median speed of movement (cm s^{-1}) were recorded based on x-y coordinates in each frame.

For all fish in the treatment groups ($n = 48$), risk-taking behaviour and sociability were initially measured at 24°C (trial 1), following which temperature was raised to 27°C (trial 2) at a rate of approximately 1°C per 10 minutes, meaning ramping occurred over 30 minutes (Figure 4.1). Fish were then given 10 minutes to settle following temperature change before the risk-taking behaviour and sociability trials were repeated. The temperature was then further increased from 27°C to 30°C at the same rate of temperature

increase, and risk-taking behaviour and sociability trials were carried out at 30°C (trial 3). Following trial completion, the central chambers were gradually cooled back to 24°C, over approximately 15 minutes.

To control for time spent in the arena, $n = 46$ (reduced from $n = 48$ due to mortality occurring between treatment and control trials being carried out; see ethical note) individuals from eight groups were used in temporal control trials. Fish came from three control groups of naïve fish that did not experience temperature treatments, and five groups (treatment groups 2, 4, 6, 7, and 8) that had previously experienced trials with temperature change (Supplementary Figure 4.1). Temporal control trials consisted of the same temporal setup as described above, including ramp periods, but temperature did not change during the “ramp” periods and was instead maintained at 24°C, i.e., trials 1, 2, and 3 occurred at 24°C (Figure 4.1). Trials were carried out in the order: treatment groups (individual trials); treatment groups (group trials); control groups (individual trials); control groups (group trials) (Supplementary Figure 4.1). Trials were arranged so that fish had a minimum of 48 hours to recover between individual and group trials, and where necessary, between temperature ramp and temporal control trials.

4.3.5. *Group behavioural trials*

To allow behaviours recorded independently of conspecifics to be linked to interactions within a group, group behavioural trials were carried out for the same fish used in individual behavioural trials. Groups in which fish were housed during routine holding were the same groups in which they were tested for group behaviour. During group trials ($n = 8$ groups of five to six individuals), the same arenas were used as for individual trials, with the opaque inserts left in so fish could not see into the adjacent chambers. Removable curved inserts were added to the corners of the central chamber to prevent fish from congregating in the corners. The central plant shelter was removed for group behavioural trials, to minimise interference during the automated tracking of fish positions. Pipes were left in place as these did not block the view of the camera (Figure 4.1). At the start of each trial, recording from the camera above the arena was started and all individuals in a group were placed into the tank in a specific order according to individual tag ID. This allowed individuals IDs to be known throughout the trial. While groups originally contained six fish, some mortality (total $n = 11$) occurred throughout the experiment. This was attributed to natural causes and tagging-related mortality (detailed below) and while fish were replaced if group size decreased below five individuals (TG3) we did not have sufficient

individuals to replace all mortalities. For this reason, TG3 contained five individuals at the time of group temperature ramp trials. Sample size for individual behavioural metrics within group trials was therefore $n = 47$. While individuals were filmed throughout the 15-minute trial, only the latter ten minutes were used in data analysis to allow fish five minutes to recover from transfer to the central chamber. During pilot trials, a 20-minute acclimation period was used, however it was observed that the fish returned to normal behaviour, i.e., regular opercular rhythm, moving around the central chamber and interacting with conspecifics, after five minutes when in groups. While groups may have varied in time taken to acclimate, all groups used in the final analysis were observed to resume normal behaviour within five minutes. Acclimation and trial time were therefore kept constant to allow trial order to be more easily accounted for in models.

All groups were placed in arenas at 24°C. For half of the groups, fish were initially filmed at 24°C (trial 1) following which temperature was ramped to 27°C (trial 2) and 30°C (trial 3) as described for individual trials, with fish given ten minutes to settle at each new temperature (Figure 4.1). To control for the effects of repeated handling during trials, the other half of groups experienced reversed temperature ramp order: fish were added to central chambers at 24°C, following which temperature was increased to 30°C over the course of one hour. Trials were then carried out as described above, with central chambers decreasing rather than increasing in temperature between trials, i.e., trial 1 was carried out at 30°C, trial 2 at 27°C, and trial 3 at 24°C.

Similarly to in individual trials, temporal control trials were carried out for group behaviour to examine the effects of time spent in the arena. These used the same groups listed above for individual temporal control trials. Control groups (CG1-3) failed to resume normal behaviour in group trials. For temporal control group trials therefore only groups that had previously experience temperature ramp trials were used in final analysis, giving $n = 5$ groups of five to six individuals. Reasons for failure to resume normal behaviour in control groups are unknown as control fish behaved normally in individual trials.

Group behavioural trials were analysed using the motion tracking software TRex (Walter & Couzin, 2021). All tracks were manually checked to ensure accurate identification at the individual level throughout, referencing the source video if necessary. The interpolation function in TRex was also activated, to allow interpolation of x and y coordinates if a track was momentarily lost. Data processing was carried out in R (version 4.5.1) (R Core Team,

2025). Measures of interindividual distance (*mean nearest neighbour distance (NND) (cm)*, *mean distance to the shoal centroid (MDCS) (cm)*), activity (*median speed (cm s⁻¹)*), polarisation (*median turning angle (TA) (°)*), *mean rescaled bearing to the nearest neighbour (°)* (MacGregor & Ioannou, 2023)), *mean heading difference from nearest neighbour (°)* and position within the group (*mean normalised distance along the group's direction of motion*) were calculated for all individuals throughout the trial. Speed, turning angle, rescaled bearing, and heading difference were only calculated when individual speed was $\geq 1 \text{ cm s}^{-1}$, as this was taken to represent active swimming. This threshold value was based on the frequency distribution of speeds, which had a mode at 1 cm s^{-1} , indicating that lower values likely reflected minimal or non-swimming movement. Mean distance along the group's direction of motion was only calculated from time points where group polarisation was greater than 0.3, i.e., when fish were swimming in approximately the same direction. To assess behaviour at the level of the whole group, median speed of the group centroid (cm s^{-1}) and mean group polarisation were also calculated for each trial. Mean group polarisation was calculated only from time points when group speed was $\geq 1 \text{ cm s}^{-1}$, i.e., when the group was swimming together and polarisation could be calculated reliably. Full details of how metrics were calculated can be found in the supplementary methods.

Due to time constraints, trials were carried out once at each temperature for each individual or group. A summary of treatments and trials is shown in Supplementary Figure 4.1.

4.3.6. Statistical analysis

4.3.6.1. PRINCIPAL COMPONENT ANALYSES

As multiple behavioural metrics were collected for each trial, we use a multivariate approach to analysis where feasible to reduce multiple comparisons and collinearity. For traits measured in individual behavioural trials, a principal component analysis (PCA) with a correlation matrix was performed on DCS, activity in sociability trials, and MDNS. This PCA was intended primarily as a dimensionality-reduction approach for analysing overall effects of temperature and time on individual behaviour while minimising multiple comparisons. Activity in risk-taking behaviour trials and thigmotaxis were modelled separately due to zero-inflation making these variables incompatible with a standard PCA (Hellton et al., 2021). The first two principal components (PCs), cumulatively explaining 83.5% of total variance, were then used as response variables to model the effects of temperature on individual behavioural traits (Supplementary Figure 4.2A). This PCA was

constructed using data from both temporal control and temperature ramp trials, to allow effects of time to be accounted for in models.

A second PCA, also using a correlation matrix, was subsequently carried out using only data from individual temperature ramp trials. As correlations among DCS, MDNS, and activity in sociability trials (Supplementary Figure 4.3A, Supplementary Table 4.1A) caused collinearity in preliminary models of behaviour in groups, this PCA was used to reduce collinearity among individual behavioural traits before these were included as explanatory variables in models of group behaviour. Because the goal in this case was to remove correlations among behavioural variables rather than reduce the total number of variables, all three resultant PCs were retained for subsequent analyses, with PCs 1, 2, and 3 explaining 52%, 29.6%, and 18.4% of the total variance respectively (Supplementary Figure 4.2B).

When modelling data from group trials, due to the large number of variables collected for individual-level behaviour within group trials (NND, mean distance to the group centroid, speed, turning angle, difference in heading, rescaled bearing, and normalised distance along group motion) and the correlations among these (Supplementary Figure 4.3B; Supplementary Table 4.1B), these variables were also reduced using another PCA. The first three components, respectively explaining 37.2%, 29.5%, and 15.1% of variance, were then used as the response variables in models of group behaviour (Supplementary Figure 4.4).

4.3.6.2. INDIVIDUAL TEMPERATURE TRIALS

To determine the effects of temperature on individual behaviour, four models were constructed on data from temperature ramp and temporal control trials. The response variables in these models were thigmotaxis, activity in risk-taking behaviour trials, and the first two principal components of the PCA constructed on DCS, MDNS, and activity in sociability trials using both temperature ramp and control data. The explanatory variables in these models were treatment (control or temperature ramp treatment), trial number as a factor, and the interaction between treatment and trial number. Trial number was included along with the interaction to separate effects of time and temperature, as all individual temperature trials were carried out in the same order. Fish ID nested within group ID was also included as a random effect. PCs 1 and 2 were modelled using linear mixed models (LMMs) in the glmmTMB package (Brooks et al., 2017), with PC1 being log-transformed

to ensure model assumptions were met. Thigmotaxis and activity in risk-taking behaviour trials were modelled using generalized LMMs (GLMMs) with zero-inflated beta distributions in the glmmTMB package (Supplementary equations 4.1-4.2) with values $< 0.3 \text{ cm s}^{-1}$ being taken as zero values in the case of activity in risk-taking behaviour trials.

4.3.6.3. GROUP TEMPERATURE TRIALS

To determine whether behavioural traits of fish in individual trials were linked to behaviour displayed by these individuals in group trials, three LMMs were constructed in glmmTMB. The response variables in these models were the first three components of the PCA carried out on individual-level behavioural variables measured in group trials, as described above. Explanatory variables were temperature as a factor, trial number as a continuous variable, standard length (mm) and the three components of the PCA carried out on individual behavioural traits (sociability, risk-taking behaviour, and activity in sociability trials) using data from temperature ramp trials only. Trial number was included as a continuous variable to reduce degrees of freedom and because we found no evidence that the effect of time was not linear, based on models constructed from temporal control data (Supplementary Table 4.2; Supplementary models 4.1-4.2). The interactions between temperature and all individual behavioural variables, and between temperature and standard length were also included in the full models. Group size as a factor (five or six), and fish ID nested within group ID were included as random effects.

To determine the effects of temperature and individual traits on group speed and polarisation, two LMMs were constructed in glmmTMB. The response variables in these models were group speed and group polarisation, with both being log transformed to ensure model assumptions were met. Explanatory variables were temperature as a factor, trial number as a continuous variable, standard length (mm) and the three components of the PCA carried out on individual behavioural traits using data from temperature ramp trials only. The interactions between temperature and all individual behavioural traits, and between temperature and standard length, were also included in the full models. Group ID and group size as a factor (five or six) were included as random effects.

For all group models, stepwise model selection was carried out using the `drop1()` function with a likelihood ratio test in the stats package to compare models without each interaction term. Interaction terms were retained if there was evidence that removing them affected the model log likelihood (Tredennick et al., 2021) at $p < 0.05$. Post-hoc analysis was then

carried out on all models in the emmeans package using a Tukey p -value adjustment for multiple comparisons (Lenth, 2025), to compare among levels of the temperature variable and any retained interactions.

For all analyses, model fit and validation of model assumptions were examined using the DHARMA package (Hartig, 2016) in R. Pseudo- R^2 with (conditional R^2 ; R^2_c) and without (marginal R^2 ; R^2_m) random effect variables were calculated for each model (Nakagawa & Schielzeth, 2013) using the MuMIn package (Bartoń, 2010). R^2 was not calculated for models with zero-inflated distributions, as R^2 does not account for zero-inflation, making results difficult to interpret.

4.3.7. *Ethical note*

All work involving live fish was carried out under personal licence (PIL) number I32381320 (UK) granted to ICT and project licence number PP2587075 (UK) granted to SSK. Licences for live animal work were granted by the UK Home Office. All procedures were approved by the University of Glasgow Animal Welfare and Ethical Review Body, Named Training and Competency Officer Dr Lesley Gilmour, and Named Veterinary Surgeon Dr Lynda Dunbar under University of Glasgow Experimental Request Form number/AWERB approval number ZRF024. Animals were sourced through a supplier verified for animal welfare by the University of Glasgow Zoological Research Facility. Animals were sourced from a reputable trader and transported under controlled conditions. The number of animals acquired was calculated to allow formation of eight groups of six fish for use in temperature trials ($n = 48$), four groups of six fish used in temporal control trials ($n = 24$), and four groups of six fish for use as stimulus shoals ($n = 24$; total $n = 96$). All individuals were adults; however exact age of individuals is unknown. Individuals were not sexed as *H. rhodostomus* do not display sex-specific external characteristics. Animals were initially housed in groups of ~50 before being divided into groups of six and placed in smaller tanks. Both small and large tanks contained gravel substrate and artificial plants to provide shelter and reduce stress. Tanks were constantly flushed with fresh water and were cleaned weekly to remove any build-up of waste and uneaten food and prevent disease. Fish were fed twice daily on flake food, and on frozen bloodworms weekly to improve dietary variation and provide a source of protein. Fish were housed in an aquarium with limited access to minimise disturbance. For all behavioural trials, fish were allowed time to settle in arenas and following temperature changes to minimise stress and facilitate the return of normal behaviour following transport to behavioural arenas. Fish

spent minimal time in behavioural arenas before being returned to holding tanks. For tagging, weighing, and measuring, fish were anaesthetised to reduce stress. Fish were supervised during recovery from anaesthesia and allowed at least 48 hours to recover from tagging prior to being used in behavioural trials. Anaesthesia using the usual recommended dose of benzocaine (5 mg l^{-1}) resulted in mortality of all individuals tagged ($n = 5$), therefore anaesthesia dose was halved (2.5 mg l^{-1}) for all remaining tagging and no further mortality following tagging was observed. Other mortality during the study was minimal ($n = 6$) and attributed to natural mortality, as fish age varied. Following trial completion, untagged stimulus fish ($n = 24$) were rehomed in line with departmental guidelines and following vet examination. Tagged treatment and control fish ($n = 61$ remaining) were Schedule 1 culled using anaesthetic overdose (benzocaine 10 mg l^{-1}).

4.4. Results

4.4.1. Principal component analyses

For individual behavioural data from temperature ramp and temporal control trials, PC1 (51.2% of variance) was found to be negatively correlated with sociability (positively correlated with DCS), activity in sociability trials, and risk-taking behaviour (MDNS) (Supplementary Figure 4.3A). Greater PC1 scores therefore indicated less-social, less-active, more risk-averse fish. PC2 (32.3%) was positively correlated strongly with MDNS and less-strongly with DCS, indicating less risk-averse, less-social fish, but was negatively correlated with activity.

For individual behavioural data from temperature ramp trials only, correlations with PC1 (52%) and PC2 (29.6%) were similar to those described above (Supplementary Figure 4.3B). PC3 (18.4%) was strongly negatively correlated with DCS and activity in sociability trials, meaning greater PC3 scores indicated fish that were more active but less social.

For the PCA of individual-level behavioural metrics within group trials, PC1 (37.2% of variance) was positively correlated with speed but negatively correlated with heading difference and turning angle; thus, higher values of PC1 indicate fast, straight, polarised swimming (Supplementary Figure 4.4). PC2 (29.5%) was positively correlated with NND and MDCS, indicating greater inter-individual distances (Supplementary Figure 4.4), and with bearing to nearest neighbour, indicating nearest neighbours were more likely found alongside rather than in front or behind. PC3 (15.1%) was negatively correlated with the distance along the group's direction of motion, so that fish near the rear of the shoal had

higher PC3 values. PC3 was also positively correlated with the bearing angle of the nearest neighbour, indicating fish swimming alongside one another (Supplementary Figure 4.4).

4.4.2. Individual temperature trials

Standard length of fish ranged from 24.1-33.4 mm with a mean $\pm$ se of 28.4 ± 0.32 (Supplementary Table 4.3). Mean standard lengths within groups were between 27-29 mm for all but two groups (TG2: 29.4 mm; CG3: 31.7 mm). Fish mass ranged from 0.284 g to 1.204 g with a mean $\pm$ se of 0.535 ± 0.024 g. Mean mass within groups ranged from 0.4-0.56 g for all but two groups (TG2: 0.808 g; CG3: 0.665 g).

Activity in risk-taking behaviour trials was greater in trial 2 of control trials (GLMM: $z = 2.481$, $p = 0.013$; Table 4.1). The zero-inflated model showed a reduction in the number of completely inactive fish (i.e., zero values) at both 27°C (temperature trial 2) (GLMM_{zi}: $z = -2.697$, $p = 0.007$) and 30°C (temperature trial 3) (GLMM_{zi}: $z = -2.738$, $p = 0.006$; Table 4.1; Figure 4.2A). While there were no effects of temperature on thigmotaxis found in the conditional model (27°C: $p = 0.735$; 30°C: $p = 0.359$), the zero-inflated model showed an increase in incidence of thigmotactic behaviour i.e., fish were less likely to spend no time near the wall, at 30°C (GLMM_{zi}: $z = -2.595$, $p = 0.009$; Table 4.1; Figure 4.2B). There was also an increase in thigmotaxis in temperature compared with control trials (GLMM_{zi}: $z = -2.240$, $p = 0.025$), and a marginally non-significant increase in thigmotaxis in trial 3 of control trials (GLMM: $z = 1.850$, $p = 0.064$). There was a marginally non-significant increase in PC1 (low sociability, activity, risk-taking) scores in trial 3 (LMM: $z = 1.847$, $p = 0.065$) and a marginally non-significant decrease at 30°C (LMM: $z = -1.874$, $p = 0.061$). Post-hoc testing showed that PC1 scores were significantly lower at 30°C (temperature trial 3) than in control trial 3 (emmeans: $z = -3.004$, $p = 0.032$), indicating increased sociability, activity, and risk-taking at high temperature in trial 3 (Table 4.1; Figure 4.2C). PC2 (high risk-taking, low sociability and activity) scores were lower in temperature ramp trials compared with temporal control trials (LMM: $z = -2.266$, $p = 0.024$), however no effect of trial number or the interaction with treatment was found (Table 4.1).

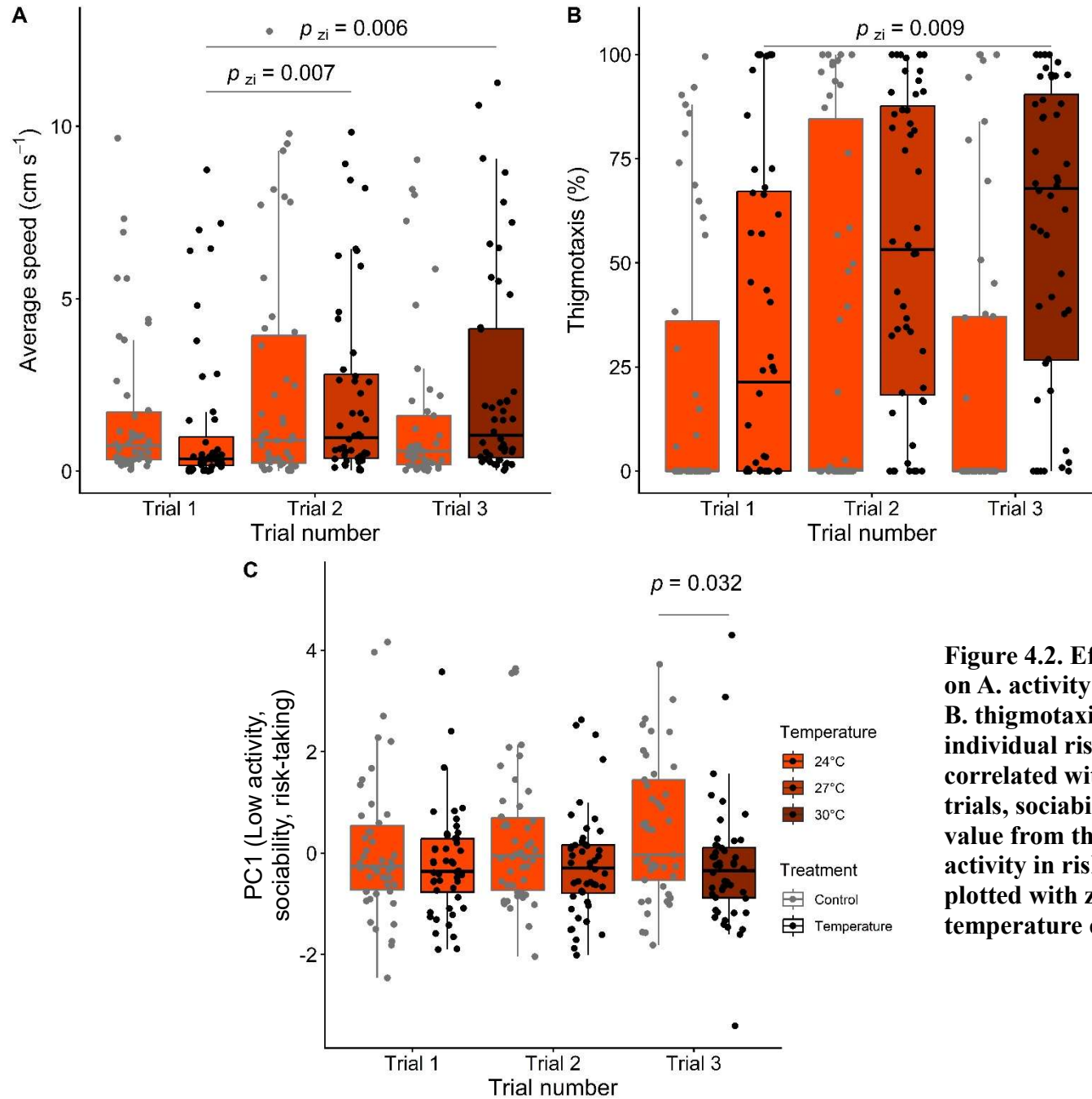


Figure 4.2. Effect of repeated trials and temperature on **A.** activity level in individual risk-taking trials; **B.** thigmotaxis (time spent near the arena wall) in individual risk-taking trials; **C.** PC1: negatively correlated with activity in individual sociability trials, sociability, and risk-taking. p_{zi} indicates the p value from the zero-inflated model (Table 4.1) as activity in risk-taking trials and thigmotaxis were plotted with zero-inflated distributions. p values for temperature effects only are shown on graphs.

Table 4.1. Factors affecting traits displayed by individuals in individual risk-taking behaviour and sociability trials. Variables with significant or marginally non-significant effects are shown in bold. * indicates significance at $p < 0.05$. ** indicates significance at $p < 0.01$. * indicates significance at $p < 0.001$. OR = Odds ratio. R^2 values represent pseudo- R^2 . R^2 values were not calculated for zero-inflated models as the effects of zero-inflation are ignored, making results difficult to interpret.**

Response variable	Explanatory variable	Estimate	Std. Error	z	p	R^2_m	R^2_c
						0.029	0.418
PC1 (Low sociability, activity, risk-taking)	Intercept	1.335	0.044	30.54	< 0.001		
	Treatment (Temperature)	-0.027	0.052	-0.513	0.608		
	Trial 2	0.051	0.050	1.036	0.300		
	Trial 3	0.092	0.050	1.847	0.065		
	Temp*Trial2	-0.058	0.069	-0.828	0.408		
	Temp*Trial3	-0.131	0.070	-1.874	0.061		
	Control Trial 2 – Temp Trial 2 (27°C)	-0.084	0.052	-2.232	0.588		
<i>Post-hoc test</i>	Control Trial 3 – Temp Trial 3 (30°C)	-0.157	0.052	-3.004	0.032*		
						0.031	0.185
PC2 (High risk-taking, low sociability, activity)	Intercept	0.044	0.811	0.054	0.957		
	Treatment (Temperature)	-0.445	0.197	-2.266	0.024*		
	Trial 2	0.041	0.187	0.219	0.827		
	Trial 3	-0.070	0.188	-0.372	0.710		
	Temp*Trial2	0.003	0.028	0.114	0.910		
	Temp*Trial3	0.126	0.261	0.481	0.631		
	Control Trial 2 – Temp Trial 2 (27°C)	-0.320	0.197	-1.626	0.581		
<i>Post-hoc test</i>	Control Trial 3 – Temp Trial 3 (30°C)	-0.178	0.197	-0.905	0.946		
Thigmotaxis (conditional model)	Intercept	-0.143	0.285	-0.502	0.615		
	Treatment (Temperature)	0.280	0.362	0.822	0.411		
	Trial 2	0.405	0.370	1.095	0.274		
	Trial 3	0.795	0.423	1.850	0.064		
	Temp*Trial2	-0.159	0.469	-0.339	0.735		
	Temp*Trial3	-0.476	0.519	-0.918	0.359		
	Intercept	0.351	0.299	1.174	0.241		
Thigmotaxis (zero-inflated model)	Treatment (Temperature)	-0.952	0.425	-2.240	0.025*		
	Trial 2	-0.526	0.421	-1.249	0.212		
	Trial 3	0.444	0.440	1.009	0.313		
	Temp*Trial2	-0.641	0.660	-0.971	0.331		
	Temp*Trial3	-1.789	0.689	-2.595	0.009**		
	Control Trial 2 – Temp Trial 2 (27°C)	OR: 0.871	0.274	-0.439	0.998		
	Control Trial 3 – Temp Trial 3 (30°C)	OR: 1.195	0.452	0.471	0.997		
<i>Post-hoc test (conditional)</i>							
<i>Post-hoc test (conditional)</i>							

Activity (risk-taking) (conditional model)	Intercept	-1.619	0.191	-8.499	< 0.001
	Treatment (Temperature)	0.047	0.251	0.186	0.852
	Trial 2	0.565	0.228	2.481	0.013*
	Trial 3	0.051	0.237	0.215	0.830
	Temp*Trial2	-0.309	0.330	-0.938	0.348
	Temp*Trial3	0.335	0.336	0.997	0.319
Activity (risk-taking) (zero-inflated model)	Intercept	-1.558	0.389	-4.006	< 0.001
	Treatment (Temperature)	1.222	0.487	2.509	0.012*
	Trial 2	0.732	0.504	1.451	0.147
	Trial 3	0.865	0.501	1.725	0.084
	Temp*Trial2	-1.861	0.690	-2.697	0.007**
	Temp*Trial3	-1.864	0.681	-2.738	0.006**
<i>Post-hoc test (conditional)</i>	Control Trial 2 – Temp Trial 2 (27°C)	OR: 1.300	0.299	1.141	0.864
<i>Post-hoc test (conditional)</i>	Control Trial 3 – Temp Trial 3 (30°C)	OR: 0.682	0.165	-1.584	0.609

4.4.3. Group temperature trials

Fish swam faster and were more polarised with nearest neighbours at 27°C (LMM_{PC1}: $z = 6.624$, $p < 0.001$) and 30°C (LMM_{PC1}: $z = 10.52$, $p < 0.001$; Table 4.2; Figure 4.3A) compared with at 24°C, and post-hoc analysis showed an increase in speed and polarisation at 30°C compared with at 27°C (emmeans_{SPC1}: $z = 3.988$, $p < 0.001$). Fish were less polarised and swam more slowly in successive trials (LMM_{PC1}: $z = -6.392$, $p < 0.001$). Inter-individual distances were reduced at 27°C (LMM_{PC2}: $z = -2.573$, $p = 0.010$; Table 4.2; Figure 4.3B) and at 30°C (LMM_{PC2}: $z = -2.032$, $p = 0.042$) but no significant difference was found between 27-30°C. Inter-individual distance was also increased in successive trials (LMM_{PC2}: $z = 9.514$, $p < 0.001$). Fish swam in a more linear spatial arrangement (i.e., one in front of the other), and were more even distributed along the group range of motion at 27°C (LMM_{PC3}: $z = -2.241$, $p = 0.025$; Table 4.2; Figure 4.3C) and at 30°C (LMM_{PC3}: $z = -2.598$, $p = 0.009$), but there was no difference between 27-30°C (Table 4.2). A negative relationship between group PC3 with individual PC2 (LMM_{PC3}: $z = -2.423$, $p = 0.015$; Figure 4.3D) indicates that fish with greater risk-taking behaviour but lower activity and sociability swam near the front of the shoal in a more linear spatial arrangement. Fish swam in a more linear spatial arrangement and were more evenly distributed throughout the group in successive trials (LMM_{PC3}: $z = -4.172$, $p < 0.001$; Table 4.2).

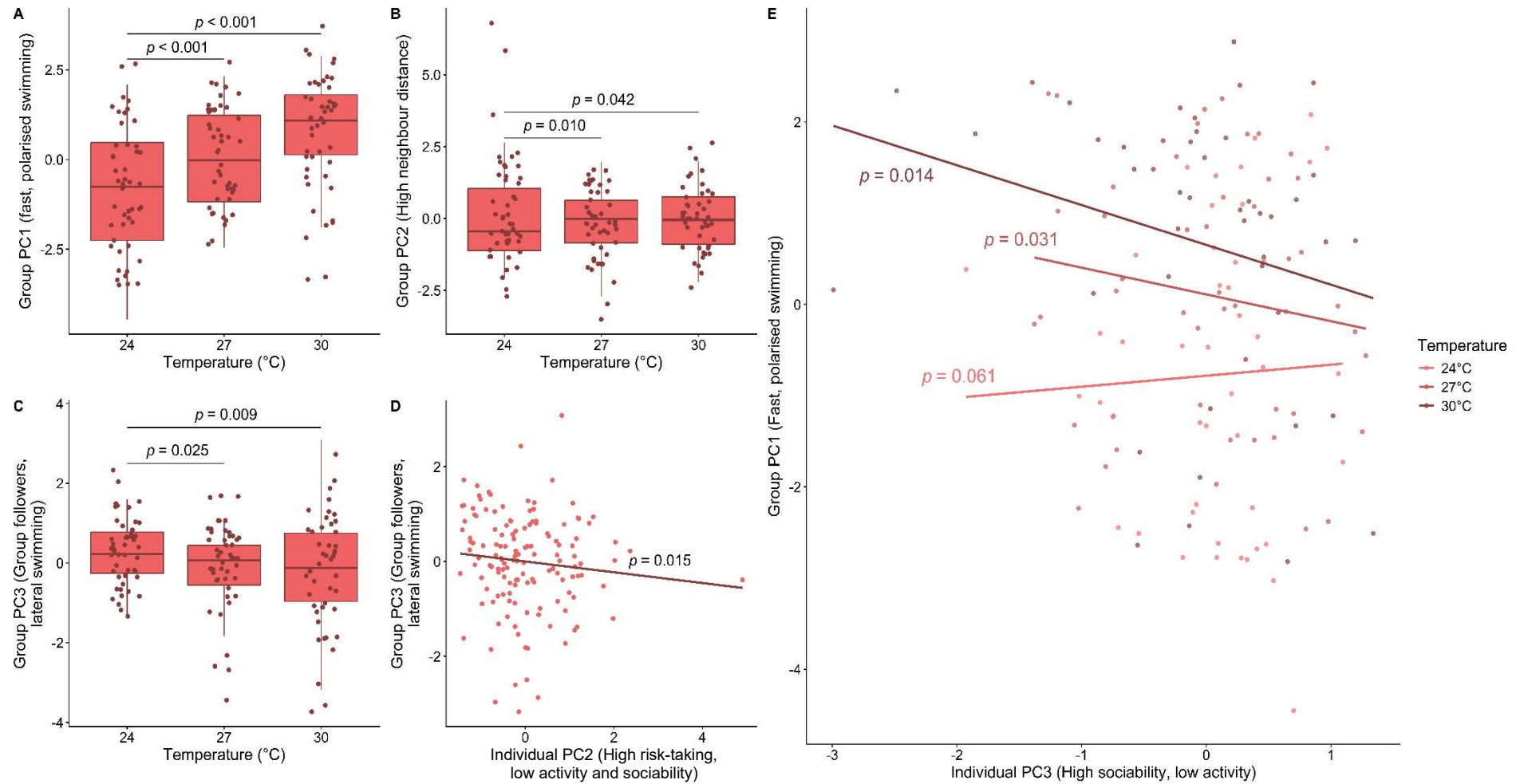


Figure 4.3A. Effect of temperature on group PC1: positively correlated with speed, negatively correlated with turning angle and heading difference to nearest neighbour, B. Effect of temperature on group PC2: positively correlated with inter-individual distance and bearing to nearest neighbour. C. Effect of temperature on group PC3: negatively correlated with distance along group range of motion, positively correlated with bearing to nearest neighbour. D. Relationship between group PC3 and individual PC2: Positively correlated with risk-taking behaviour, negatively correlated with activity and sociability. E. Effect of temperature on the relationship between group PC1 and individual PC3: positively correlated with sociability, negatively correlated with activity in sociability trials.

There was a marginally non-significant positive relationship between individual PC3 (social, less-active fish) and swimming speed and polarisation in group trials at 24°C (LMM_{PC1}: $z = 1.873$, $p = 0.061$; Table 4.2; Figure 4.3E). The interaction between individual PC3 and temperature was retained in the PC1 model (LRT = 6.226, $p = 0.044$) and had a negative relationship with PC1 at 27°C (LMM_{PC1}: $z = -2.159$, $p = 0.031$; Table 4.2; Figure 4.3E) and 30°C (LMM_{PC1}: $z = -2.461$, $p = 0.014$). The positive effect of temperature on speed and polarisation of individuals in groups was therefore reversed in fish that were social but less active (Table 4.2). Fish standard length had no effect on any metric of individual behaviour in a shoal (Table 4.2). A visual representation summarising the relationships between individual and group dynamics across temperatures is shown in Figure 4.4.

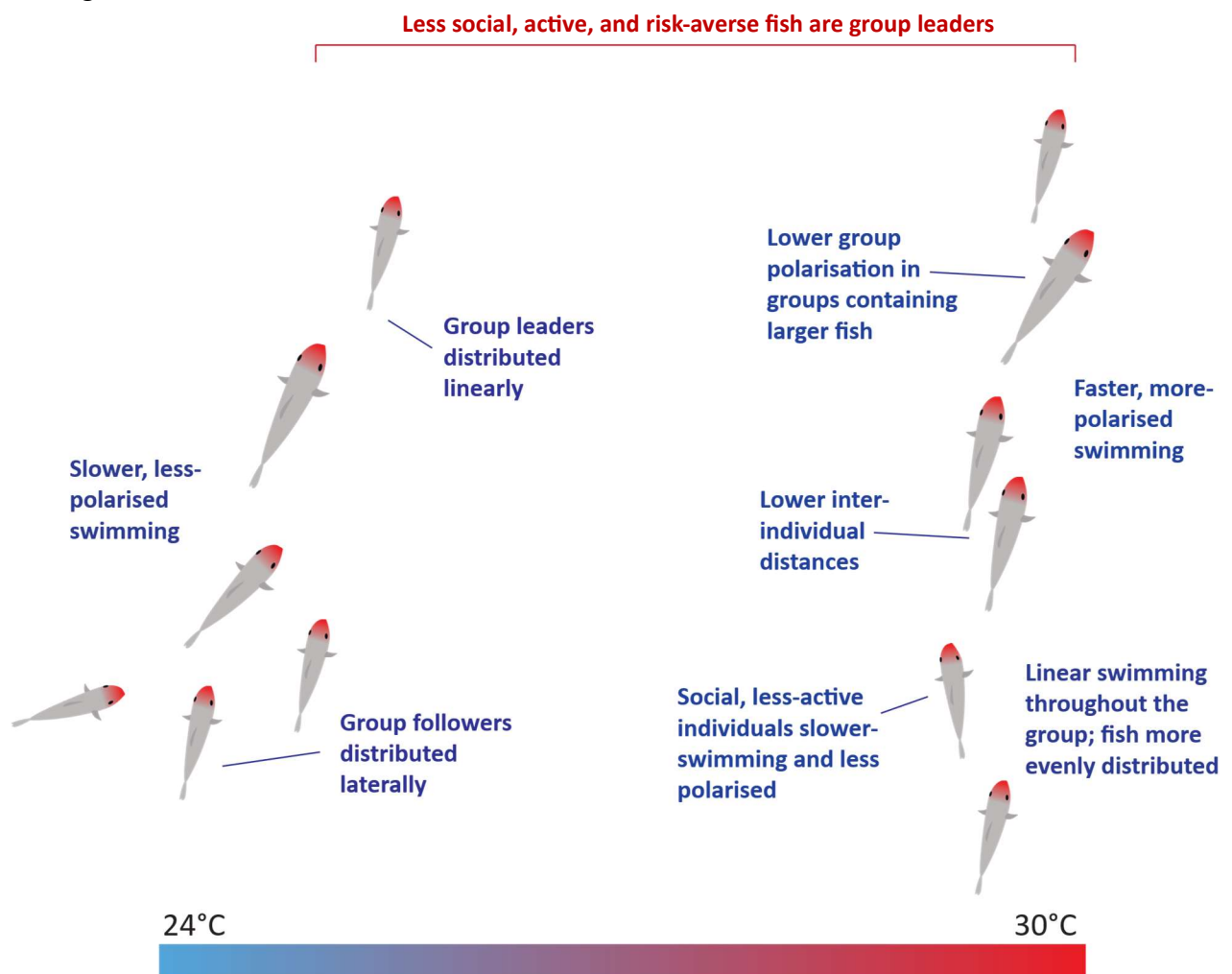


Figure 4.4. Diagram showing differences and similarities in group dynamics at control (left) and elevated (right) temperatures. Similarities in group dynamics across temperature conditions are shown in **red**; dynamics that were changed at high temperatures are shown in **blue**.

Table 4.2. Results of general linear mixed models of factors affecting traits displayed by individuals during group trials. Variables with significant or marginally non-significant effects are shown in bold. * indicates significance at $p < 0.05$. ** indicates significance at $p < 0.01$. * indicates significance at $p < 0.001$. R^2 values represent pseudo- R^2 .**

Response variable	Explanatory variable	Estimate	Standard error	z value	p value	R^2_m	R^2_c
						0.195	0.833
PC1 (fast, polarised, straight-line swimming)	Intercept	0.458	1.119	0.410	0.682		
	Low sociability, activity, risk-taking (PC1)	-0.034	0.058	-0.597	0.551		
	High risk-taking, low sociability, activity (PC2)	0.012	0.068	0.181	0.856		
	High sociability, low activity (PC3)	0.349	0.186	1.873	0.061		
	Standard length (mm)	-0.013	0.036	-0.350	0.726		
	27°C	0.905	0.137	6.624	< 0.001***		
	30°C	1.452	0.138	10.52	< 0.001***		
	Trial number	-0.440	0.069	-6.392	< 0.001***		
	PC3*27°C	-0.479	0.222	-2.159	0.031*		
	PC3*30°C	-0.535	0.217	-2.461	0.014*		
<i>Post-hoc test</i>	27-30°C	0.547	0.137	3.988	< 0.001***		
<i>Post-hoc test</i>	PC3*27-30°C	-0.056	0.198	-0.294	0.954		
						0.204	0.743
PC2 (spread out, unpolarised)	Intercept	-3.462	1.417	-2.444	0.015		
	Low sociability, activity, risk-taking (PC1)	-0.040	0.066	-0.605	0.545		
	High risk-taking, low sociability, activity (PC2)	-0.092	0.079	-1.160	0.246		
	High sociability, low activity (PC3)	-0.179	0.110	-1.627	0.104		
	Standard length (mm)	0.080	0.049	1.634	0.102		
	27°C	-0.387	0.151	-2.573	0.010*		
	30°C	-0.310	0.153	-2.032	0.042*		
	Trial number	0.725	0.076	9.514	<0.001***		
<i>Post-hoc test</i>	27°C - 30°C	0.078	0.152	0.511	0.866		
						0.122	0.648
	Intercept	1.133	1.371	0.827	0.408		

PC3 (swimming alongside, back of group)	Low sociability, activity, risk-taking (PC1)	-0.110	0.062	-1.782	0.075
	High risk-taking, low sociability, activity (PC2)	-0.169	0.070	-2.423	0.015*
	High sociability, low activity (PC3)	-0.119	0.096	-1.241	0.215
	Standard length (mm)	-0.012	0.048	-0.257	0.797
	27°C	-0.296	0.132	-2.241	0.025*
	30°C	-0.347	0.134	-2.598	0.009**
	Trial number	-0.278	0.067	-4.172	<0.001***
<i>Post-hoc test</i>	27°C - 30°C	-0.052	0.133	-0.380	0.920

The centroid of the shoal moved faster at 27°C (LMM: $z = 9.114$, $p < 0.001$; Table 4.3; Figure 4.5A) and 30°C (LMM: $t = 14.66$, $p < 0.001$) compared with at 24°C, and at 30°C compared with at 27°C (emmeans: $z = 5.654$, $p < 0.001$). Speed was reduced, however, in successive trials (LMM: $z = -11.95$, $p < 0.001$). Group polarisation was increased at both 27°C (LMM: $z = 2.306$, $p = 0.021$; Table 4.3; Figure 4.5B) and 30°C (LMM: $z = 3.832$, $p < 0.001$) compared with at 24°C, and at 30°C compared with at 27°C (emmeans: $z = 3.425$, $p = 0.002$). Polarisation also declined with successive trials (LMM: $z = -11.53$, $p < 0.001$). Groups comprised of social, less-active fish moved faster in group trials at 24°C (LMM: $z = 2.817$, $p = 0.005$; Table 4.3; Figure 4.5C). This relationship was altered at high temperatures, however, with groups containing social, less-active individuals moving more slowly at 30°C (LRT = 9.124, $p = 0.01$; LMM: $z = -3.179$, $p < 0.001$; Table 4.3; Figure 4.5C). At 27°C, groups containing social, less-active individuals still moved faster, however this trend was reduced ($z = -2.078$, $p = 0.038$; Figure 4.5C). Behavioural traits of individuals within groups had no effect on group polarisation (Table 4.3), however, there was a positive effect of standard length on group polarisation at 24°C (LMM: $z = 2.097$, $p = 0.036$; Figure 4.5D). The interaction between standard length and temperature was also retained in the group polarisation model (LRT = 7.762, $p = 0.021$). Polarisation was reduced in shoals containing larger fish at 30°C (LMM: $z = -3.014$, $p = 0.003$).

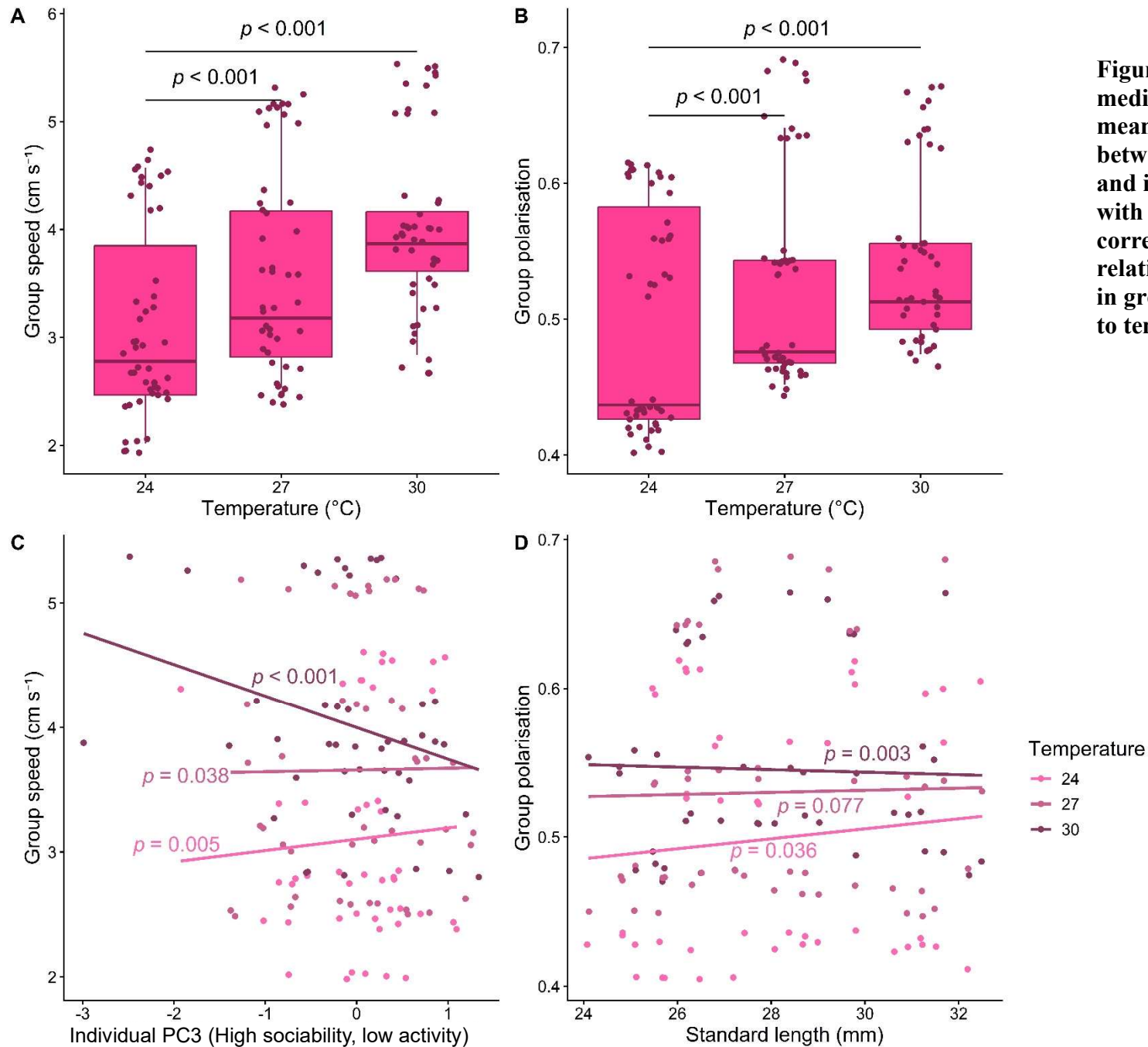


Figure 4.5. Effect of temperature on A. median speed of the group centroid, B. mean group polarisation, C. the relationship between median speed of the group centroid and individual PC3: negatively correlated with activity in sociability trials, positively correlated with sociability, and D. the relationship between standard length of fish in groups and group polarisation, according to temperature treatment.

Table 4.3. Results of general linear mixed models of factors affecting group speed and polarisation during group trials. Variables with significant or marginally non-significant effects are shown in bold. * indicates significance at $p < 0.05$. ** indicates significance at $p < 0.01$. * indicates significance at $p < 0.001$. R^2 values represent pseudo- R^2 .**

Response variable	Explanatory variable	Estimate	Standard error	z value	p value	R^2_m	R^2_c
						0.300	0.885
Group speed	Intercept	1.296	0.125	10.35	< 0.001		
	Low sociability, activity, risk-taking (PC1)	-0.004	0.007	-0.572	0.567		
	High risk-taking, low sociability, activity (PC2)	-0.002	0.009	-0.257	0.797		
	High sociability, low activity (PC3)	0.065	0.023	2.817	0.005**		
	Standard length (mm)	0.001	0.004	0.261	0.794		
	27°C	0.173	0.019	9.114	< 0.001***		
	30°C	0.280	0.019	14.66	< 0.001***		
	Trial number	-0.114	0.010	-11.95	< 0.001***		
	PC3*27°C	-0.061	0.029	-2.078	0.038*		
	PC3*30°C	-0.088	0.028	-3.179	0.001**		
<i>Post-hoc test</i>	27°C - 30°C	OR: 0.898	0.017	5.654	< 0.001***		
<i>Post-hoc test</i>	PC2*27-30°C	0.028	0.024	1.148	0.485		
						0.173	0.898
Group polarisation	Intercept	-0.768	0.095	-8.09	< 0.001		
	Low sociability, activity, risk-taking (PC1)	-0.001	0.003	-0.242	0.809		
	High risk-taking, low sociability, activity (PC2)	0.000	0.004	0.071	0.943		
	High sociability, low activity (PC3)	0.008	0.006	1.428	0.153		
	Standard length (mm)	0.006	0.003	2.097	0.036*		
	27°C	0.270	0.117	2.306	0.021*		
	30°C	0.450	0.117	3.832	< 0.001***		
	Trial number	-0.057	0.005	-11.53	< 0.001***		
	27°C*SL	-0.007	0.004	-1.767	0.077		
	30°C*SL	-0.013	0.004	-3.014	0.003**		
<i>Post-hoc test</i>	27°C - 30°C	OR: 0.967	0.009	3.425	0.002**		
<i>Post-hoc test</i>	27-30°C*SL	-0.005	0.004	-1.262	0.417		

SL = Standard length (mm); OR = Odds ratio.

4.5. Discussion

Abiotic stressors such as temperature are increasingly recognised as critical drivers of animal behaviour, yet how individual-level thermal responses give rise to emergent group-level dynamics in gregarious species remains poorly understood (Tiddy, Munson, et al., 2024). Our results reveal that influence of individual behavioural traits on group dynamics are modulated by temperature in *H. rhodostomus*. Notably, individuals that were less social, less active, and had a greater tendency to risk-taking when alone tended to position themselves at the front of groups, possibly giving these individuals a greater role in initiating movement (N. Miller et al., 2013; Nakayama et al., 2012). Overall, individuals and groups swam faster and were more polarised at higher temperatures. Group structure changed as temperature increased, however, with more linear positioning of individuals throughout the group, and social, less-active fish swimming more slowly. Speed of the group centroid was also reduced in groups containing social, less-active individuals at 27-30°C, indicating that temperature alters how traits scale to group-level performance. These findings highlight that both individual traits and environmental conditions influence collective behaviour, improving our understanding of how social fish species might respond to acute thermal stress.

Increased temperatures are often associated with higher metabolic rates in ectotherms (Clarke & Johnston, 1999; Nati et al., 2018; Pilakouta et al., 2020), possibly leading to greater activity in mobile species such as fish (Bartolini et al., 2015). This is consistent with our results wherein faster swimming speeds were found at higher temperatures in individual and group behavioural trials. Increased activity may lead to greater risk-taking behaviour (Ioannou, 2017; Killen, Fu, et al., 2016; McKenzie et al., 2015; Metcalfe et al., 2016) and reduced sociability (Angiulli et al., 2020; Cooper et al., 2018; reviewed in Tiddy, Munson, et al., 2024), both as a function of increased movement and due to changes in social drive (Garrido et al., 2016; Killen, Cortese, et al., 2021). While we found increased risk-taking behaviour (mean distance to shelter) at 30°C, fish were also generally closer to the arena walls (thigmotaxis) at this warm temperature. Increased thigmotaxis in this case may therefore be a by-product of increased activity, with individuals moving more being more likely to spend time near the chamber walls, without this necessarily representing a reduced tendency for risk-taking behaviour. It should be noted that R^2_m values, i.e., the amount of variation explained by fixed model effects of treatment, trial, and their interaction, were low compared with variation explained by the random effect of individual fish identity ($R^2_m - R^2_c$) in models for individual behavioural traits. This indicates

a strong influence of individual identity on behaviour over that of the thermal environment, i.e., potentially high cross-context repeatability (Killen, Adriaenssens, et al., 2016). Repeatability itself was not examined in the present study, however, due to lack of repeated samples across thermal conditions. Similarly high levels of behavioural variation explained by individual identity *versus* environmental effects have been found in, for example, guppies *Poecilia reticulata* (O'Neill et al., 2018) and cod *Gadus morhua* (Villegas-Ríos et al., 2018), though further study of behavioural repeatability is needed in *H. rhodostomus*.

The observed increase in sociability at high temperatures may indicate that even when moving more, *H. rhodostomus* prioritise proximity to a social group over exploring, foraging, or attempting to escape acute thermal stress. The majority of previous studies have found either a negative effect or no effect of temperature on sociability in fish (Angiulli et al., 2020; Cooper et al., 2018; Mehdi et al., 2022; Pilakouta et al., 2023; Tiddy, Munson, et al., 2024). One study on meagre *Argyrosomus regius* reported increased sociability with warming, but this was not accompanied by increased activity (Maulvault et al., 2018). It should be noted, however, that the majority of studies have focused on acclimated exposure to temperature change, rather than short-term thermal stress (Tiddy, Munson, et al., 2024). Acute temperature change may be less likely to elicit a reduction in sociability, as gregarious fish often move closer together when stressed, and conspecific presence has been found to have a “calming” effect on individuals (Nadler et al., 2016; Pintos et al., 2024). Interestingly, Cooper et al. (2018) found that acutely exposed stickleback *Gasterosteus aculeatus* were less likely to alter space use to spend time with a shoal placed in warmer water (i.e., reduced sociability) in a temperature choice assay. Responses to acute temperature change may therefore vary among species and possibly depending on factors such as individual temperature preference (Cooper et al., 2018). Even when fish are allowed time to acclimate, temperature may also amplify the effects of other acute stressors (Munson et al., 2024). Weetman et al. (1999) found that guppies preferred smaller shoals when acclimated at high temperatures but switched this preference when exposed to a predation threat, an effect that was not found at low temperatures. While acclimated exposure is highly relevant to many ecosystems, understanding the behavioural impacts of short-term thermal stress is also key for freshwater species living in variable environments, such as Amazonian tetra species (Campos et al., 2017; Marshall et al., 2011).

It has previously been shown that individual traits can impact group dynamics (e.g., Jolles et al., 2017), however our study is the first to show that while behavioural traits of known individuals may scale up to affect group dynamics, this is in some cases temperature dependent. Fish that displayed lower sociability and activity in sociability trials, and higher risk-taking behaviour tended to swim at the front of the group in group trials (PC3; Figure 4.3). This finding is consistent with previous work on fish, which found that less-social (Bevan et al., 2018; Jolles et al., 2017) and less risk-averse (Bevan et al., 2018; Harcourt et al., 2009; Nakayama et al., 2012, 2016) individuals were more likely to swim at the front of shoals and/or initiate movements. This effect was not dependent on temperature in the present study, though fish in groups swam more linearly at higher temperatures (PC3). Increased movement linearity may be due to increased swimming speed, as found in rainbowfishes *Melanotaenia* spp. (M. I. A. Kent et al., 2019). In the present study, fish generally increased in speed and polarity with nearest neighbours at higher temperatures; however, we found the relationship between speed and polarity of swimming of individuals in groups (PC1) and temperature to be dependent on individual traits. Fish with high sociability but low activity in sociability trials reduced their speed relative to shoalmates and increased turning angle and bearing to nearest neighbours at higher temperatures (Figure 4.3A; Figure 4.4). Speed of the group centroid also increased with temperature, but decreased at higher temperatures in groups containing social, less-active individuals (Figure 4.5A). Increased speed of movement within shoals with temperature at both the individual and group levels has been found by several studies (Bartolini et al., 2015; Davis et al., 2019; Luo et al., 2024); however, modulation of this effect according to the behavioural traits of individuals within groups has previously lacked empirical evidence. The effects of temperature and other abiotic factors on the links between levels of social behaviour is an important area for further study in fish, given the prevalence of gregarious behaviour across species and life stages.

While our results show evidence that individual behavioural traits may interact with the effects of temperature when fish are placed in groups, the mechanisms for this remain unclear. Fish often swim faster with increasing temperature below a critical threshold due to higher metabolic activity (Luo et al., 2024; Zeng et al., 2009), however this response has been found to vary both among (Gomez-Maldonado & Camacho-Cervantes, 2022; Luo et al., 2024) and within species (Biro et al., 2010; Johansen et al., 2014). In the present study, more-social, less-active individuals differed in their temperature-related activity response when in groups. This may be an effect of physiological limitation, if these fish were unable

to keep up with faster-moving conspecifics at higher temperatures (Johansen & Jones, 2011). As we did not measure physiological thermal tolerance or swimming performance, however, this is purely speculative. Alternatively, some individuals may reduce activity at higher temperatures as an energy-saving strategy. Johansen et al. (2014) found reduced spontaneous swimming activity in coral trout *Plectropomus leopardus* at increased temperatures, an effect attributed to energy-saving behavioural plasticity. Some fish species have previously been found to conform to groupmates' swimming speeds (Jolles et al., 2018), however, in some cases prioritising this over individual preferred swimming speeds (Tiddy et al., 2025). In addition, groups in the present study did not lose polarisation or increase interindividual distances at high temperatures as would be expected if some individuals were unable or did not choose to swim with the group. A recent study found temperature to modulate links between metabolic rate and individual behaviour in sheepshead minnow *Cyprinodon variegatus* (Schumm et al., 2026), while individual variation in plastic metabolic response to low temperatures was not reflected in behavioural variation in cunner *Tautoglabrus adspersus* (Norin et al., 2024). Factors other than increased metabolic rate may help to determine behaviour under varying thermal conditions, therefore. As we cannot rule out an effect of physiological limitation in the present study, however, it would be highly beneficial for future studies to measure metabolic as well as behavioural responses to temperature at the individual and group levels.

Interestingly, the effects of individual behavioural traits on speed, individual polarity with nearest neighbours, and within-group positioning were not present for individual distance to nearest neighbours or to the group centroid (inter-individual distances), or for polarisation at the group level. Group polarisation is strongly linked to swimming speed (M. I. A. Kent et al., 2019), and both were found to increase with temperature in the present study (Figure 4.5). Despite intra-individual and intra-group variation in swimming speed and group dynamics across temperatures, though, the effect of temperature on group polarisation was not dependent on individual behavioural traits. There was, however, a negative effect of standard length of individuals within groups on polarisation at higher temperatures. As larger fish tend to be less agile (Jolles, King, et al., 2020) and have a larger repulsion distance (Romenskyy et al., 2017) larger fish may struggle to maintain polarisation with other shoal members at the higher speeds observed in this study at higher temperatures. In the case of inter-individual distances, previous studies of temperature on shoaling have often found fish to move apart as swimming speeds increase (Bartolini et al.,

2015; Davis et al., 2019), though recent studies have shown that fish are sometimes able to remain close to shoalmates despite moving faster (Kuruvilla et al., 2023; Luo et al., 2024). In *H. rhodostomus* we found lower inter-individual distances at high temperatures, despite increased activity. *H. rhodostomus* have been found to perform well in shoaling tests involving a visual stimulus (light-dark gradient), due to their ability to individually sense and respond to stimuli (Puckett et al., 2018). While our assays did not involve such a gradient, it is possible that the shoaling performance of *H. rhodostomus* allows them to maintain low inter-individual distances at high speeds despite variation in individual behavioural responses to temperature.

Time, i.e., the number of successive trials to which fish had been subjected, had a significant effect on group speed and polarisation, and on various individual-level metrics measured within group trials. It is possible therefore that additional handling affected fish behaviour (Philippe et al., 2023), however as the direction of temperature ramping was reversed in half of group trials our models are still able to detect effects of temperature independent of time. It has previously been found that group movements in fish may become less coordinated and more variable over time even without a handling stimulus (MacGregor & Ioannou, 2021), so the observed effect may have been found regardless. In individual trials, while effects of time were found on thigmotaxis, activity in risk-taking trials, and PC1, effects of treatment, i.e., temperature ramps in successive trials were also found on these variables. This indicates that while changes in behaviour over time occurred in control trials, responses in some temperature trials differed significantly (Table 4.1), showing evidence for effects of thermal stress on individual-level behavioural traits.

4.6. Conclusions

As environmental extremes become more common, predicting their ecological impacts for social species will require understanding not only how temperature affects individuals, but also how effects on individuals alter interactions within groups. In *H. rhodostomus* acute warming showed both independent and trait-dependent effects on social behaviour: activity, sociability, and risk-taking behaviour increased in isolated fish, and higher activity also emerged in groups at elevated temperatures, but in a manner that depended on the individual behavioural traits of constituent group members. Moreover, individual traits were linked to group position and behavioural role, and the traits that best predicted these roles differed in some cases among thermal environments. These results suggest that thermal stress does not simply change mean behaviour but can alter how behavioural

variation among individuals is expressed within groups. More broadly, our findings highlight that forecasting the effects of warming on social species will require moving beyond individual-level responses alone and considering how temperature modifies the contribution of different individuals to collective behaviour.

Chapter 5

Hypoxia alters the link between individual behavioural variation and collective dynamics in a social fish

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5.1. Abstract

As rising temperatures impact aquatic ecosystems, hypoxia is an increasing threat to organisms. Many fishes are dependent on dissolved oxygen to meet their metabolic needs and are therefore vulnerable to changes in oxygen level. Hypoxia has been found to have metabolic and neurosensory effects on fish, which may lead to disruption of adaptive behaviours. While there is significant evidence that hypoxia reduces group cohesion in fish, evidence for changes to individual sociability and other behaviour traits is lacking. Here, we aimed to investigate the effects of hypoxia on social behaviour at the group and individual level in *Hemigrammus rhodostomus*. We also sought to determine whether hypoxia affects the association between individual traits and group-level behaviours, or dynamics within the group. We tested individual social and risk-taking behaviour in *H. rhodostomus* at three levels of oxygen: 100% (normoxia), 70% (mild hypoxia) and 30% (severe hypoxia). We then placed these fish in groups of six and used high-resolution tracking to analyse both group-level behaviour and behaviour of individuals with known traits, under the same treatments. Fish were less active under low oxygen in both individual and group trials. In group trials, shoals were less polarised but more cohesive, particularly

for larger fish, under severe hypoxia. Risk-taking behaviour in individual trials may modulate the response to hypoxia in group trials, likely through differences in activity level response. Our study reveals how individual behavioural traits contribute to group dynamics under varying conditions.

5.2. Introduction

The increasing severity of climate change and anthropogenic pollution is a growing problem for many ecosystems, leading to changes in abiotic conditions. Low levels of dissolved oxygen, or hypoxia, as a result of increased temperatures and eutrophication is a key concern in aquatic environments (Gattuso et al., 2015; Graham et al., 2025; Levin et al., 2015). Changes in abiotic conditions such as hypoxia frequently have strong effects on behaviour and physiology, even at sublethal levels (Domenici et al., 2017). As environmental change becomes more widespread and extreme, understanding plastic responses and evolutionary adaptations to these stressors at the individual level has become increasingly important to ecological understanding and conservation efforts. Just as important, however, is the ability to contextualise these adaptations above the individual level, and to understand how individual-level adaptations translate to changes at the level of social groups. This approach is vital to our interpretation of individual-level data and is therefore an area of increasing interest in ecological research (Jolles, King, et al., 2020).

Hypoxia is a significant stressor in aquatic ecosystems, the incidence of which has been growing in recent years (Graham et al., 2025; Pezner et al., 2023). Hypoxia, generally defined as occurring when water oxygen content is $\leq 30\%$ air saturation (Cook et al., 2014; Domenici et al., 2017; Tiddy, Munson, et al., 2024), has a range of effects on aquatic organisms. In extreme cases, hypoxia or anoxia, meaning a complete lack of oxygen, may result in suffocation and death for organisms (Domenici et al., 2017). At less severe levels, hypoxia may have sublethal effects (Heuer & Grosell, 2014). Hypoxia can affect metabolic and neural functioning in fish and other aquatic organisms (Domenici et al., 2007; Lucon-Xiccato et al., 2014; Schellart & Wubbels, 1998), with carry-over effects on behaviour, including increases or reductions in activity associated with attempts to escape hypoxic conditions (Domenici et al., 2000) or conserve oxygen, respectively [Click or tap here to enter text.](#) (Herbert & Steffensen, 2005; Killen et al., 2012). Hypoxia may also affect space use, such as increases in airbreathing (Killen et al., 2018; Pineda et al., 2020) or aquatic surface respiration (Mandic & Regan, 2018) to access oxygen. Behaviours such as these

may allow organisms to cope with unfavourable conditions while avoiding or buffering physiological stress arising from these conditions (Domenici et al., 2017).

Behavioural responses to or constraints induced by stressors may, however, interfere with key adaptive behaviours such as social behaviour, and the ways in which behaviour scales from individual to group levels. In gregarious species, social behaviour is advantageous for predator protection, foraging success, and reproduction (Ioannou, 2017; Marras et al., 2015; Pitcher et al., 1982). The dynamics of social groups may, however, depend on the behavioural traits of individuals within the group and the roles that these individuals take. Jolles *et al.* (2017) found that more social stickleback *Gasterosteus aculeatus* swam more slowly when in a group and swam closer to nearest neighbours, while more active, less social individuals tended to swim at the front of moving groups. Tendency for risk-taking behaviour may also have an effect on within-group positioning, with fish that are less risk-averse being more likely to lead groups or initiate movements (Bevan et al., 2018; Nakayama et al., 2012, 2016). Changes to social behaviour arising from stressors such as hypoxia may therefore occur at both the individual and group levels, and stressors may modulate the relationship between individual behavioural traits and group dynamics. For example, in a gregarious species that tends to be less cohesive under hypoxic conditions, sociability in individuals may no longer function as a predictor of cohesive group behaviour under hypoxic conditions. Various studies have investigated the effects of hypoxia on group cohesion, meaning the tendency to shoal together, in fish species (Alfonso et al., 2020; Cook et al., 2014; Domenici et al., 2002; Hayes et al., 2019; Moss & McFarland, 1970; Tiddy, Munson, et al., 2024). The effects of hypoxia on individual behavioural traits such as sociability, and the role of these traits in determining group dynamics in response to hypoxia, however, are less well-studied (Sommer-Trembo et al., 2017; Tiddy, Munson, et al., 2024). For gregarious animals, understanding how links between individual behavioural traits and group dynamics may vary according to abiotic conditions is key to predicting impacts of abiotic stressors on species.

Despite the increasing relevance of studying the impact of abiotic stressors on behaviour, the links between behavioural traits of known individuals and their interactions with conspecifics in a group is yet to be studied in the context of hypoxia. The present study compared behaviour of individuals and groups in a model species, rummy-nose tetra *Hemigrammus rhodostomus*. These fish were chosen as they are a schooling species that do not display aggressive or territorial behaviour towards conspecifics (Jiang et al., 2017).

We aimed to investigate the effects of hypoxia on risk-taking (isolated individuals), sociability (where a conspecific shoal was visible) and activity level in individual rummy-nose tetra. Risk-taking behaviour was measured here as tendency to leave a shelter (mean distance to a shelter). We then quantified the joint effects of hypoxia and individual-level traits on the same individuals in free-swimming group trials. We measured shoaling behaviour at both the individual level (proximity to their nearest neighbour and the group centroid, angular direction of individuals' nearest neighbour, difference in heading with the nearest neighbour, relative position of the individual in the group's direction of motion) and group level (the speed of the group centroid and polarisation of the group).

5.3. Methods

5.3.1 Study animals

Wild-caught *Hemigrammus rhodostomus* were supplied by The Trop Co. and delivered to the Zoological Research Facility (ZRF), Graham Kerr Building, University of Glasgow, on 16/10/2023. Fish were allowed to recover from transit in one of two large (280 l) tanks each containing ~50 individuals. After one week, groups of six fish were randomly selected and housed in smaller (10 l) tanks. Of these groups, eight were used as treatment groups, while four were used as stimulus shoals. The remaining three groups were designated as control groups. Originally, four control groups were allocated, however some control individuals had to be used to replace individuals in other groups, including one treatment group (TG3), due to mortality ($n = 11$ in total, attributed to natural mortality ($n = 6$) and tagging, detailed below). Groups were held at 24°C and 100% oxygen saturation. After the experiment, untagged stimulus fish were rehomed following vet examination and approval of the animal welfare officer. Tagged treatment and control fish were euthanized using anaesthetic overdose (benzocaine 10 mg l⁻¹). Study fish had a mean ($\pm$ standard error) standard length of 28.4 ± 0.34 mm (range 24.1 - 33.4 mm) and a mean mass of 0.535 ± 0.024 g (range 0.284 - 1.204 g). Full per-group fish size data is shown in Supplementary Table 5.1. As temperature and hypoxia exposures were originally intended to be carried out as a single experiment, fish used in hypoxia trials were the same as those used in the temperature trials described in Chapter 4, with temperature trials being carried out prior to temporal control trials. The temporal control data used for Chapters 4 and 5 is the same.

5.3.2 Tagging

Following group allocation, individuals in treatment and control groups were individually tagged using elastomer tags. The first group of individuals were anaesthetised for tagging

using 5 mg l⁻¹ benzocaine solution, however this dose caused 80% mortality (mortality $n = 5$) and dose was therefore halved to 2.5 mg l⁻¹ for the remainder of the groups. No further mortality during or immediately after tagging was observed. Individuals were weighed (mass in grams) and standard length (SL) in millimetres was measured after tagging.

5.3.3 *Experimental setup*

Experimental arenas consisted of four behavioural arenas lined with white paper to improve video quality and provide a uniform environment. Each arena was divided into three parts using transparent PVC dividers, with a smaller chamber (11.5 x 36.5 cm) at each end and a larger, central chamber (32.8 x 36.5 cm). Aquarium-safe silicon was used to seal dividers, preventing water exchange between chambers and meaning stimulus shoals would not experience hypoxia. Opaque white PVC plastic inserts were placed next to the transparent dividers during risk-taking behaviour trials, to prevent visual access to the stimulus shoal. Chambers were filled with water to a depth of 6 cm. Each arena contained a water inlet and outlet, which were connected to a sump at 24°C (one sump per arena) via two Eheim 10 l min⁻¹ pumps. Sump temperature was regulated via a heating pipe connected to an Inkbird thermostat, the sensor of which was placed in the behavioural arena (Supplementary Figure 5.1). An air stone connected to a nitrogen gas cannister via a solenoid valve was also placed in the sump. The solenoid valve was connected to a FireSting oxygen probe, with the sensor placed in the behavioural arena. The FireSting was connected to an OxyReg oxygen regulator. This allowed the nitrogen flow and therefore the level of oxygen in the arena to be regulated to within +/-5%. To reduce stress to focal fish, shelter was provided in the form of an artificial plant placed in the centre of the arena, and two upright opaque pipes placed either side of the plant. To provide shelter to stimulus fish, artificial plants were also placed in the smaller chambers.

5.3.4 *Individual behavioural trials*

For the first trial of each day, stimulus individuals were randomly allocated to one side of each arena; the side on which shoals were placed was then alternated throughout the day. During risk-taking behaviour trials, opaque inserts prevented focal individuals from seeing the conspecifics in the adjacent chamber. Sealing the transparent dividers also prevented olfactory cues from attracting fish to the side containing the shoal. Fish were initially allowed 30 minutes of free swimming to acclimate to the arena and resume normal behaviour. Fish were then filmed from above using a GoPro Hero 6 Black in linear mode with a frame rate of 25 fps and 1080p resolution for ten minutes.

Videos of individual behavioural trials were processed using the motion tracking software EthoVision (Noldus et al., 2001). In risk-taking behavioural trials, the following individual behavioural metrics, hereafter referred to as individual behavioural traits or individual traits, were extracted using the x and y coordinates of each fish in each frame of the video (25 frames per second): mean distance to nearest shelter (cm; MDNS); percentage of time spent near the chamber wall (thigmotactic behaviour); and mean speed of movement (cm s^{-1}).

Immediately after the end of risk-taking behaviour trials, the opaque inserts on each side of the central chamber were removed, allowing fish visual access to the stimulus shoal. Fish were allowed five minutes to recover from this disturbance, following which social behaviour was filmed from above for ten minutes using the same protocol as in risk-taking behaviour trials. As described above, mean distance to the conspecific shoal (cm) and mean speed of movement (cm s^{-1}) were calculated for each trial using EthoVision (Noldus et al., 2001).

Three oxygen treatments were applied to all treatment individuals ($n = 44$) for individual behavioural trials. These treatments were 100% (control level), 70%, and 30%. Risk-taking and sociability were initially measured at 100% O_2 , following which oxygen level was reduced to 70% at a rate of approximately 10% per 10 minutes, so that ramping occurred over 30 minutes. Fish were then given 10 minutes to settle at the new oxygen level. Risk-taking and sociability trials were then carried out at the new oxygen level as described above. This process was repeated, further reducing the O_2 saturation from 70% to 30% over ~40 mins. Following trial completion, fish were moved directly back into 100% O_2 saturated water.

To control for the effect of time spent in the arena and repeated exposure, $n = 46$ fish (greater than for hypoxia trials due to mortality, see above) from eight groups, consisting of three control groups that did not experience treatments, and five of the treatment groups, were used in temporal control trials. These consisted of the same time period spent in the arena as in the hypoxia trials, with the same behavioural trial protocols applied (i.e., trials were repeated three times as described above), however conditions did not change during ramp periods (Figure 5.1). Conditions were instead maintained under ambient conditions, i.e., trials 1, 2, and 3 occurred at 24°C and 100% oxygen saturation. Individuals from

treatment groups 2, 4, 6, 7, and 8 underwent control trials prior to hypoxia ramp trials; this was necessary due to logistical and time constraints, and group and individual identity were included in models as a random effect.

5.3.5 *Group behavioural trials*

The same arenas described above were used for group trials, with opaque panels left in so fish could not see into the adjacent chambers. Curved inserts were attached to the corners of the arena, so that fish did not congregate in corners. The central plant shelter was removed as it blocked the view of the camera making individual fish difficult to identify. Pipes were left in but moved to the very centre of the arena to avoid blocking the camera. At the start of each trial, the camera was switched on, and individuals were placed into the tank in a specific order according to individual tag ID, allowing individual identification at all points during the trial. Individuals were filmed throughout the 15-minute trial; however, the first five minutes were treated as a recovery period from handling and only data from the final ten minutes was used.

During group trials, oxygen was ramped following the initial trial in the same way, and fish were also given 10 minutes to settle. Fish were then captured and re-released into the tank after filming was started, as described above, at the start of trials at each oxygen concentration. To control for the effects of repeated handling during trials, half of the group trials (treatment groups 2, 3, 5, and 6) were carried out with oxygen treatments in the order described above, while the other half (treatment groups 1, 4, 7, and 8) were carried out in the reverse order (30%, 70%, 100%; Figure 5.1). Fish in the latter groups were added to behavioural arenas at 100% O₂, following which oxygen was reduced to 30% over the course of 70 mins. Trials were then carried out as described above, with arenas increasing rather than decreasing in O₂ saturation between trials. To re-oxygenate the water in these reversed ramps, an additional air stone connected to an air supply was added to the sump during oxygen ramps.

Temporal control trials were also carried out to account for time spent in the arena in group trials, using the same groups from which fish were taken for individual temporal control trials. As described above, trials were repeated three times for each group with conditions maintained at 100% oxygen and 24°C. While fish from control groups behaved normally in individual temporal control trials, control groups failed to resume normal behaviour in group trials and were therefore excluded from group trial analyses. The final sample sizes

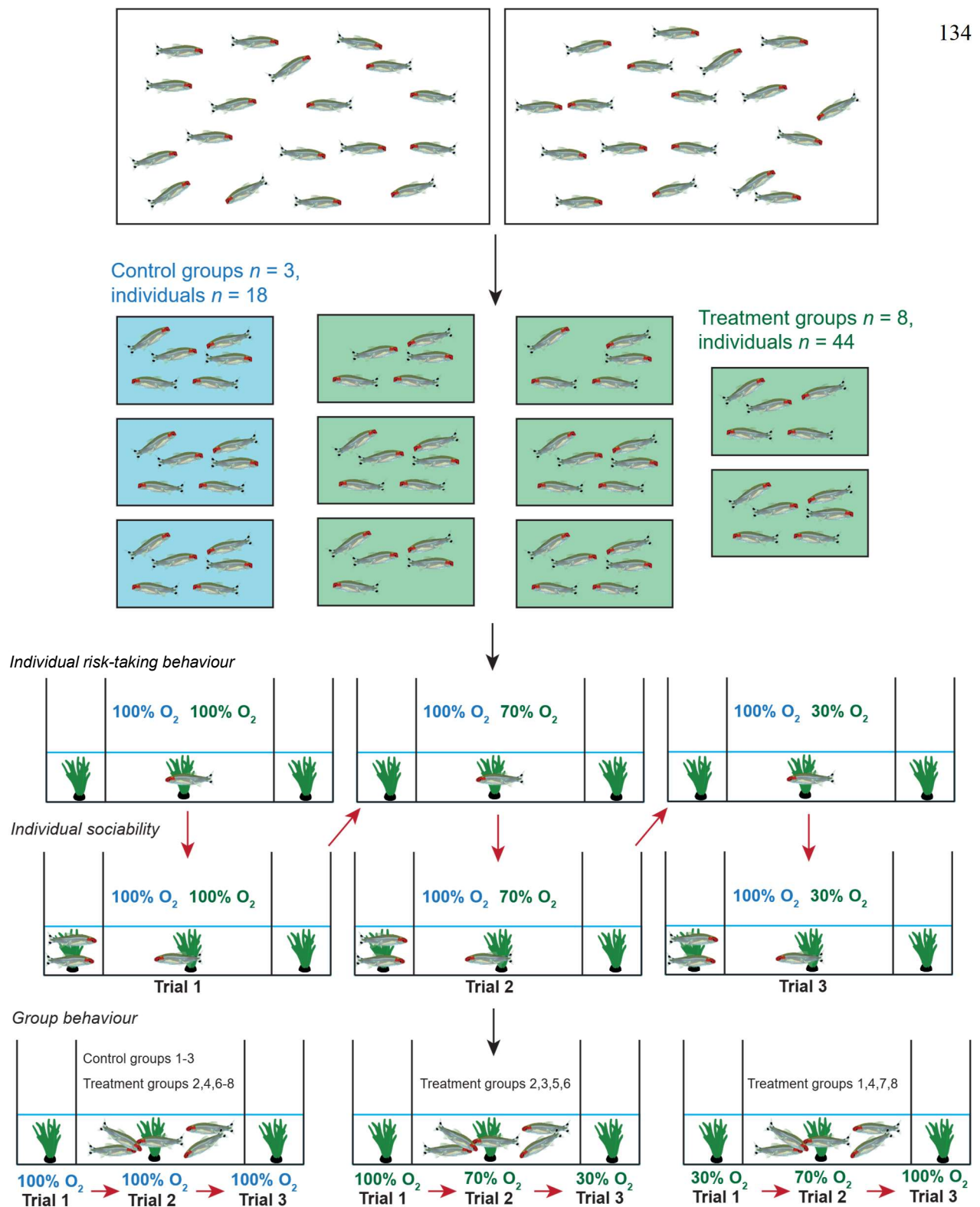


Figure 5.1. Diagram showing progression of fish through individual and group behaviour trials under different conditions of oxygen concentration. Blue writing indicates conditions experienced by control fish; green writing indicates conditions experienced by treatment fish in hypoxia trials. Black arrows indicate transfers between tanks or experiments, i.e., procedures carried out on different days. Red arrows indicate transitions between trials occurring sequentially, i.e., on the same day. Solid lines in trial diagrams indicate opaque walls; dashed lines indicate transparent barriers (sociability trials). Treatment groups 2, 4, 6, 7, and 8 underwent control trials prior to treatment trials. Tanks and experimental arenas are not shown to scale. Group trial data from control groups was excluded therefore final control trial group $n = 5$ and individual $n = 28$.

for behaviour at the group and individual levels in group temporal control trials were therefore $n = 5$ and $n = 28$, respectively.

Group behavioural trials were analysed using the motion tracking software TRex (Walter & Couzin, 2021). To ensure that individuals were correctly identified throughout videos, and to prevent identification errors if fish crossed over each other, TRex tracks were carefully checked, with reference to the original video if necessary. Where fish ID following a crossover event was not immediately clear, individuals were identified based on size, elastomer tags if these were visible in the video, and trajectory during the crossover event. The interpolation function in TRex was also activated, to allow interpolation of x and y coordinates if a track was momentarily lost.

Data processing was carried out in R version 4.3.3. (R Core Team, 2025) to calculate parameters for all individuals in each group. For each individual in each trial, interindividual distance (*mean nearest neighbour distance (NND; cm)*, *mean distance to the centre of the shoal (MDCS; cm)*), activity (*median speed (cm s⁻¹)*), polarisation (*median turning angle (TA; °)*, *mean rescaled bearing to nearest neighbour (°)*, *mean heading difference from nearest neighbour (°)*), and position within the group (*mean normalised distance along the group's direction of motion*) were calculated. Median speed, turning angle, rescaled bearing, and heading difference were only calculated when individual speed was $\geq 1 \text{ cm s}^{-1}$, indicating that fish were swimming. Distance along the group motion was only calculated where group polarisation was ≥ 0.3 , indicating unidirectional swimming. In addition, group-level measures of activity (*median speed of the group centroid (group speed; cm s⁻¹)*) and polarisation (*mean group polarisation*) were calculated for each trial. Group polarisation was calculated only from time points when group speed was $\geq 1 \text{ cm s}^{-1}$. Full details of how each metric was calculated are given in the supplementary methods.

5.3.6. Statistical analysis

5.3.6.1. PRINCIPAL COMPONENT ANALYSES

All data analysis was carried out in R version 4.5.2 (R Core Team, 2025). Due to a correlation between sociability and activity in sociability trials which caused collinearity in some models (Supplementary Figure 5.2A; Supplementary Table 5.2A), a principal component analysis (PCA) with a correlation matrix was performed on individual sociability (distance to a conspecific shoal) and activity level (mean speed of movement).

As both of the resultant principal components (PCs) explained >25% of the variance (Supplementary Figure 5.3) and the goal was to solve multicollinearity rather than reducing the number of variables, both PCs were used as explanatory variables in models of group behaviour.

In group trials, due to the large number of variables collected for individual behaviour within these trials (NND, mean distance to the group centroid, speed, turning angle, difference in heading, rescaled bearing, and normalised distance along group motion) and the correlations among these (Supplementary Figure 5.2B; Supplementary Table 5.2B), these variables were summarised using a PCA. The first three components, cumulatively explaining 78.9% of variance (Supplementary Figure 5.4), were then used as the response variables in the models of group behaviour.

5.3.6.2. INDIVIDUAL HYPOXIA TRIALS

All models were constructed using the glmmTMB package (Brooks et al., 2017). To determine the effects of hypoxia on individual behaviour, five models were constructed on data from hypoxia ramp trials and data from temporal control trials. The response variables in these models were MDNS, thigmotaxis, mean speed of movement in risk-taking behaviour trials, mean speed of movement in sociability trials, and DCS. The explanatory variables were treatment (hypoxia or control), trial number as a factor (1, 2, 3), and the interaction between treatment and trial number. The interaction was included to determine effects of hypoxia independently of time, as all individual trials were carried out with oxygen level decreasing. Fish ID nested within group ID was also included as a random effect. MDNS, activity in sociability trials, and DCS were modelled using linear mixed models (LMMs), with DCS being log transformed to meet model assumptions. Thigmotaxis and activity in risk-taking behaviour trials were modelled using generalized linear mixed models (GLMMs) with zero-inflated beta distributions, following transformation according to Supplementary Equations 5.1 and 5.2. Post-hoc analysis was then carried out on all models using the emmeans package with a Tukey adjustment (Lenth & Piaskowski, 2025) to show pairwise comparisons between control and hypoxia trials.

5.3.6.3. GROUP HYPOXIA TRIALS

To determine whether behavioural traits of fish in individual trials were linked to behaviour at the individual level in group trials, three models were constructed. The response variables in these models were the first three components of the PCA carried out

on individual-level behavioural variables in group trials, as described above. Group PCs 2 and 3 were modelled using LMMs, while PC1 was modelled using a GLMM with a beta distribution. PC1 was transformed according to Supplementary Equation S3 to allow this. To determine the effects of hypoxia and traits of individual fish in groups on group speed and polarisation, two LMMs were constructed. The response variables in these models were speed of the group centroid and group polarisation, respectively. Both speed of the group centroid and group polarisation were log transformed to meet model assumptions.

Explanatory variables in group models were individual PCs 1 and 2, risk-taking behaviour (MDNS), standard length of the fish, oxygen level as a factor, and trial number as a continuous variable. Trial number was included as a continuous variable as analysis of temporal control trial data indicated effects of trial number but did not show any indication that these were not linear (Supplementary models S5.1-5.2, Supplementary Table 5.3). The interactions between oxygen level and fish behavioural traits and standard length were also included in the full models. Model selection was then carried out using the “dredge” function in the MuMIn package to compare models with all possible combinations of interaction effects (Bartoń, 2010). The best fit model was selected based on AIC and model Akaike weight, i.e., the model with the lowest AIC value and therefore highest Akaike weight was selected (Wagenmakers & Farrell, 2004). Post-hoc analysis was then carried out on all models using the emmeans package with a Tukey adjustment (Lenth & Piaskowski, 2025) to compare among levels of the hypoxia variable and any retained interactions.

Following the original recommendations of Fisher (1922), we consider p-values as a continuous indicator of the strength of evidence against the null hypotheses being true, and use the language suggested by Muff et al. (2022) when discussing results.

That model assumptions were met for all models was verified using the model diagnostics package DHARMA (Hartig, 2016), and response variables were transformed as described above if necessary to meet model assumptions. Pseudo- R^2 with and without random effect variables were calculated for models without zero-inflated distributions using the MuMIn package (Bartoń, 2010). Pseudo- R^2 was not calculated for zero-inflated models as the effects of zero-inflation are ignored and values would therefore not be accurate. All graphs were plotted in R using the ggplot2 (Wickham, 2016) and cowplot (Wilke, 2015) packages.

5.4. Results

5.4.1. Principal component analyses

In the PCA of sociability and activity in individual sociability trials, PC1 (71.9% of variance) was positively correlated with sociability (lower distances to the conspecific shoal) and activity (Supplementary Figure 5.3), while PC2 (28.1%) was positively correlated with sociability but negatively correlated with activity. For the PCA of individual behavioural metrics within group trials, PC1 (35.8%) was positively correlated with turning angle and heading difference but negatively correlated with speed, indicating slow, unpolarised swimming (Supplementary Figure 5.4). PC2 (27.5%) was positively correlated with MDCS and NND, indicating greater inter-individual distances, i.e., reduced cohesion (Supplementary Figure 5.4). PC3 (15.6%) was negatively correlated with distance along group motion but positively correlated with bearing to nearest neighbour, representing fish swimming alongside one another near the back of the shoal (Supplementary Figure 5.4).

5.4.2. Individual hypoxia trials

There was no evidence for a change in mean distance to the nearest shelter (MDNS) with either oxygen level or trial number (Table 5.1). Thigmotaxis, i.e., the time spent near the chamber wall, was increased in hypoxia compared to control trials in the zero-inflated model (GLMM_{zi}: $z = -4.133$, $p < 0.001$; Table 5.1). There was no effect of the interaction between treatment and trial number; however, there was weak evidence for a positive effect of trial number on thigmotaxis (GLMM: $z = 1.758$, $p = 0.079$). In temporal control risk-taking behaviour trials, there was moderate evidence for increased activity in trial 2 (GLMM: $z = 2.977$, $p = 0.003$; Table 5.1) and weak evidence for reduced activity in trial 3 (GLMM_{zi}: $z = 1.725$, $p = 0.084$). There was also weak evidence for increased activity in hypoxia compared with control risk-taking behaviour trials at 100% oxygen (GLMM: $z = 1.823$, $p = 0.068$; Table 5.1) but reduced activity at 70% (GLMM: $z = -1.819$, $p = 0.069$; Figure 5.2A) and 30% O₂ (LMM: $z = -1.681$, $p = 0.093$; Figure 5.2A). Pairwise comparisons between control and hypoxia trials were non-significant, however (Table 5.1). Activity in sociability trials was reduced at 30% O₂ ($z = -3.265$, $p = 0.001$; Table 5.1; Figure 5.2B) compared with control conditions (emmeans: $z = 3.217$, $p = 0.016$). DCS was increased in trial 3, indicating reduced sociability (LMM: $z = 2.708$, $p = 0.007$; Table 5.1), but there was no effect of oxygen level.

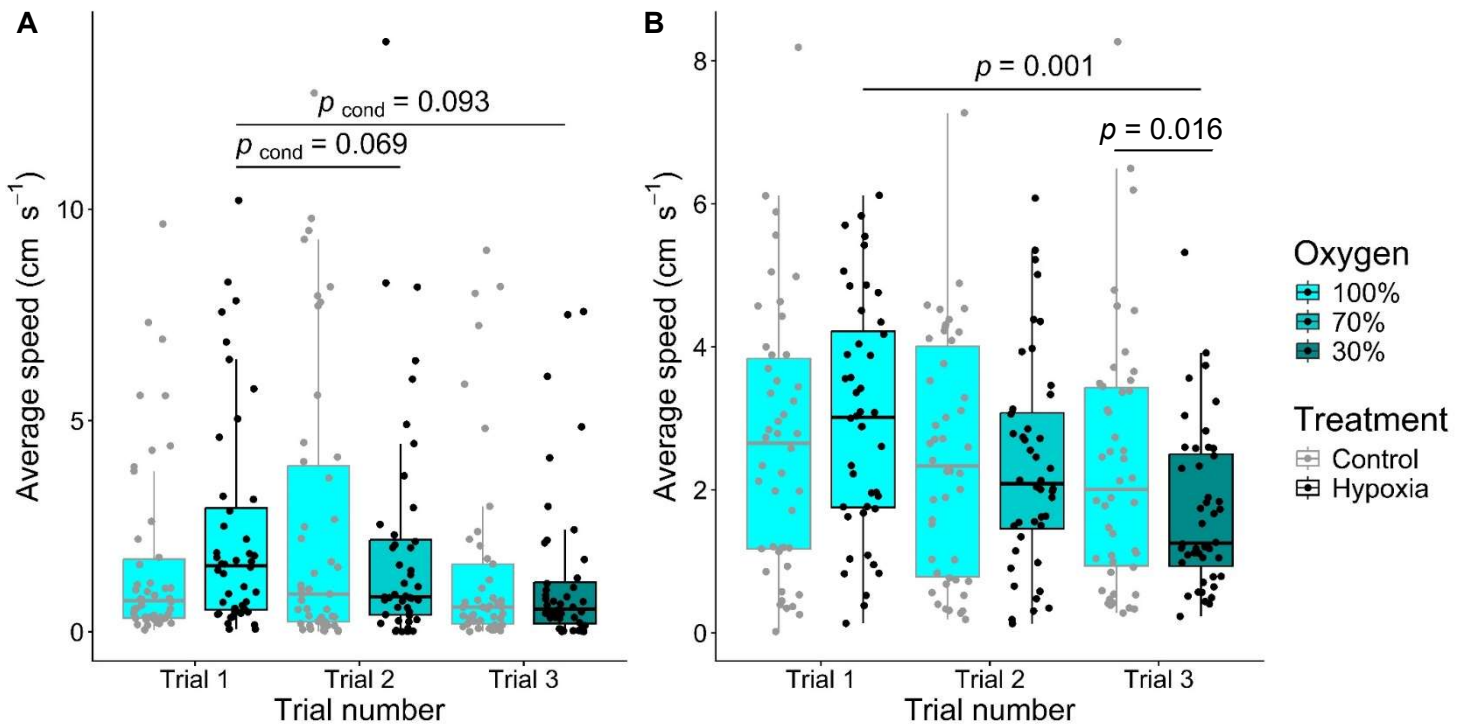


Figure 5.2 Effect of oxygen concentration and repeated trials on **A.** activity level (mean swimming speed) in risk-taking behaviour trials and **B.** activity level in sociability trials. p_{cond} indicates a p value from a conditional model output

Table 5.1. Results of (generalized) linear mixed models of factors affecting traits displayed by individuals in individual risk-taking (MDNS, thigmotaxis, activity (no shoal)) and sociability (activity (with shoal), DCS, sociability score, preferred zone) trials. Variables with evidence for an effect at $p < 0.1$ are shown in bold. * indicates significance at $p < 0.05$, ** indicates significance at $p < 0.01$, and *** indicates significance at $p < 0.001$. OR = odds ratio. R^2 values represent pseudo- R^2 . R^2 values were not calculated for zero-inflated models as effects of zero-inflation are ignored so results would not be accurate.

Response variable	Explanatory variable	Estimate	Std. Error	z value	p	R^2_m	R^2_c
MDNS	Intercept	2.179	0.244	8.935	< 0.001	0.006	0.172
	Hypoxia	-0.077	0.309	-0.249	0.803		
	Trial 2	-0.004	0.286	-0.013	0.989		
	Trial 3	-0.212	0.288	-0.735	0.462		
	Trial 2*Hypoxia	0.001	0.409	0.002	0.999		
	Trial 3*Hypoxia	-0.025	0.410	-0.062	0.951		

<i>Post-hoc test</i>	Control Trial 2 – Temp Trial 2 (27°C)	0.076	0.309	0.247	0.999		
<i>Post-hoc test</i>	Control Trial 3 – Temp Trial 3 (30°C)	0.102	0.310	0.330	0.999		
Thigmotaxis (conditional model)	Intercept	-0.061	0.311	-0.196	0.844		
	Hypoxia	0.300	0.375	0.800	0.424		
	Trial 2	0.559	0.400	1.397	0.162		
	Trial 3	0.802	0.456	1.758	0.079		
	Trial 2*Hypoxia	-0.370	0.495	-0.749	0.454		
	Trial 3*Hypoxia	0.029	0.544	0.052	0.958		
Thigmotaxis (zero- inflated model)	Intercept	0.351	0.299	1.173	0.241		
	Hypoxia	-2.197	0.532	-4.133	< 0.001***		
	Trial 2	-0.526	0.421	-1.249	0.212		
	Trial 3	0.444	0.440	1.009	0.313		
	Trial 2*Hypoxia	0.318	0.772	0.411	0.681		
	Trial 3*Hypoxia	0.304	0.712	0.426	0.670		
<i>Post-hoc test (conditional)</i>	Control Trial 2 – Temp Trial 2 (27°C)	OR: 1.073	0.369	0.206	0.999		
<i>Post-hoc test (conditional)</i>	Control Trial 3 – Temp Trial 3 (30°C)	OR: 0.720	0.294	-0.803	0.967		
Activity_{ns} (conditional model)	Intercept	-1.919	0.187	-10.25	< 0.001***		
	Hypoxia	0.396	0.217	1.823	0.068		
	Trial 2	0.633	0.213	2.977	0.003**		
	Trial 3	0.095	0.222	0.426	0.670		
	Trial 2*Hypoxia	-0.530	0.291	-1.819	0.069		
	Trial 3*Hypoxia	-0.527	0.314	-1.681	0.093		
Activity_{ns} (zero inflated model)	Intercept	-1.558	0.389	-4.006	< 0.001***		
	Hypoxia	-0.744	0.653	-1.140	0.254		
	Trial 2	0.732	0.504	1.451	0.147		
	Trial 3	0.865	0.501	1.725	0.084		
	Trial 2*Hypoxia	0.347	0.811	0.428	0.669		
	Trial 3*Hypoxia	0.457	0.801	0.571	0.568		
<i>Post-hoc test (conditional)</i>	Control Trial 2 – Temp Trial 2 (27°C)	OR: 1.143	0.241	0.634	0.989		
<i>Post-hoc test (conditional)</i>	Control Trial 3 – Temp Trial 3 (30°C)	OR: 1.140	0.275	0.542	0.994		
Activity_s	Intercept	2.748	0.233	11.81	< 0.001***	0.053	0.658
	Hypoxia	0.248	0.231	1.077	0.281		
	Trial 2	-0.216	0.212	-1.019	0.308		
	Trial 3	-0.308	0.212	-1.450	0.147		

	Trial 2*Hypoxia	-0.448	0.303	-1.476	0.140		
	Trial 3*Hypoxia	-0.990	0.303	-3.265	0.001**		
<i>Post-hoc test</i>	Control Trial 2 – Temp Trial 2 (27°C)	0.199	0.231	0.865	0.955		
<i>Post-hoc test</i>	Control Trial 3 – Temp Trial 3 (30°C)	0.742	0.231	3.217	0.016*		
						0.050	0.377
DCS	Intercept	0.338	0.069	4.916	< 0.001***		
	Hypoxia	-0.064	0.086	-0.748	0.454		
	Trial 2	0.085	0.081	1.052	0.293		
	Trial 3	0.219	0.081	2.708	0.007**		
	Trial 2*Hypoxia	0.020	0.116	0.173	0.863		
	Trial 3*Hypoxia	0.085	0.116	0.734	0.463		
<i>Post-hoc test</i>	Control Trial 2 – Temp Trial 2 (27°C)	0.044	0.086	0.515	0.996		
<i>Post-hoc test</i>	Control Trial 3 – Temp Trial 3 (30°C)	-0.021	0.086	-0.241	0.999		

MDNS = Mean distance to nearest shelter; DCS = Distance to conspecific shoal; Activity_{ns} = speed in individual risk-taking trials; Activity_s = speed in individual sociability trials

5.4.3. Group hypoxia trials

The models for group PCs 1 (ΔAIC from next-best model = 1.77; Akaike weight = 0.38) and 3 (ΔAIC = 0.25; Akaike weight = 0.18) retained the interaction between MDNS (risk-taking behaviour) and oxygen level (Table 5.2), while the model for group PC2 retained the interaction between standard length and oxygen level (ΔAIC = 0.59; Akaike weight = 0.19).

Fish swam more slowly and were less polarised at 30% O₂ compared with 100% O₂ (GLMM_{PC1}: $z = 4.526$, $p < 0.001$) and 70% O₂ (emmeans_{PC1}: $z = 3.578$, $p = 0.001$; Table 5.2; Figure 5.3A). There was moderate evidence that PC1 scores increased with increasing values of individual PC2, indicating that social, less active fish swam more slowly and were less polarised with neighbours (GLMM_{PC1}: $z = 2.169$, $p = 0.030$; Table 5.2; Figure 5.3B). There was also moderate evidence that the effect of low oxygen on PC1 was reduced in fish with greater risk-taking behaviour at 30% O₂ (GLMM_{PC1}: $z = -2.045$, $p = 0.041$; Table 5.2; Figure 5.3C). Evidence for an effect of hypoxia alone on group PC2 was weak in the main model (Table 5.2), however post-hoc testing revealed a significant reduction in inter-individual distances at 30% compared with 100% (emmeans_{PC2}: $z = -$

4.730, $p < 0.001$; Table 5.2; Figure 5.3D) and 70% O₂ (emmeans_{PC2}: $z = -4.573$, $p < 0.001$). There was moderate evidence that inter-individual distances (group PC2) decreased with increasing body size at 30% O₂ (LMM_{PC2}: $z = -2.147$, $p = 0.032$), meaning that larger fish were closer together under hypoxia (Table 5.2; Figure 5.3E). There was weak evidence that fish may have been more evenly distributed in shoals and swam more linearly, i.e., directly in front of or behind nearest neighbours, at 70% (LMM_{PC3}: $z = -1.938$, $p = 0.053$; Table 5.2; Figure 5.3F) and 30% O₂ (LMM_{PC3}: $z = -1.756$, $p = 0.079$) compared with normoxia. There was also weak evidence, however, for an effect on PC3 of the interaction between oxygen level and MDNS at 70% (LMM_{PC3}: $z = 1.836$, $p = 0.066$; Table 5.2; Figure 5.3F) and 30% O₂ (LMM_{PC3}: $z = 1.724$, $p = 0.085$), indicating that fish displaying greater risk-taking behaviour were more likely to swim near the back of the shoal, and to swim alongside conspecifics, at low O₂. There was moderate evidence for increased speed and polarisation in successive trials (GLMM_{PC1}: $z = -2.405$, $p = 0.016$; Table 5.2) and strong evidence that interindividual distances increased in successive trials (LMM_{PC2}: $z = 5.722$, $p < 0.001$; Table 5.2).

Table 5.2. Results of linear mixed models modelling variables affecting traits displayed by individuals during group trials. Variables with evidence for an effect at $p < 0.1$ are shown in bold. * indicates significance at $p < 0.05$, ** indicates significance at $p < 0.01$, and * indicates significance at $p < 0.001$. OR = Odds Ratio. R² values represent pseudo-R².**

Response variable	Explanatory variable	Estimate	Std. Error	z value	p	R ² _m	R ² _c
						0.214	0.864
PC1 (slow, unpolarised)	Intercept	-0.729	0.601	-1.213	0.225		
	High sociability, high activity (PC1)	-0.018	0.041	-0.451	0.652		
	High sociability, low activity (PC2)	0.130	0.060	2.169	0.030*		
	MDNS (cm)	0.007	0.042	0.161	0.872		
	Standard length (mm)	0.011	0.019	0.550	0.582		
	70%	-0.101	0.185	-0.544	0.586		
	30%	0.776	0.171	4.526	< 0.001***		
	Trial number	-0.113	0.050	-2.271	0.023*		
	MDNS*70%	0.025	0.067	0.379	0.705		
	MDNS*30%	-0.130	0.063	-2.045	0.041*		
<i>Post-hoc test</i>	70%-30% O₂	OR: 0.627	0.082	3.578	0.001**		

<i>Post-hoc test</i>	70-30% O₂*MDNS	-0.155	0.071	-2.172	0.076		
						0.257	0.587
PC2 (High inter-individual distances)	Intercept	-3.190	2.058	-1.550	0.121		
	High sociability, high activity (PC1)	0.029	0.097	0.295	0.768		
	High sociability, low activity (PC2)	0.125	0.149	0.839	0.401		
	MDNS (cm)	-0.052	0.063	-0.826	0.409		
	Standard length (mm)	0.085	0.071	1.189	0.234		
	70%	1.691	2.301	0.735	0.463		
	30%	3.887	2.299	1.690	0.091		
	Trial number	0.636	0.097	6.552	<0.001***		
	SL*70%	-0.065	0.082	-0.793	0.428		
	SL*30%	-0.175	0.082	-2.147	0.032*		
<i>Post-hoc test</i>	70%-30% O₂	-0.903	0.197	-4.573	<0.001***		
<i>Post-hoc test</i>	70%-30% O ₂ *SL	-0.110	0.081	-1.357	0.364		
						0.061	0.514
PC3 (swimming alongside at the back of the shoal)	Intercept	0.479	1.531	0.313	0.755		
	High sociability, high activity (PC1)	0.074	0.084	0.881	0.378		
	High sociability, low activity (PC2)	-0.072	0.134	-0.535	0.592		
	MDNS (cm)	-0.037	0.079	-0.462	0.644		
	Standard length (mm)	-0.015	0.054	-0.288	0.773		
	70%	-0.588	0.303	-1.938	0.053		
	30%	-0.519	0.296	-1.756	0.079		
	Trial number	0.058	0.079	0.738	0.461		
	MDNS*70%	0.208	0.113	1.836	0.066		
	MDNS*30%	0.194	0.112	1.724	0.085		
<i>Post-hoc test</i>	70%-30% O ₂	0.037	0.161	0.228	0.972		
<i>Post-hoc test</i>	70-30% O ₂ *MDNS	-0.015	0.117	-0.124	0.992		

MDNS = Mean distance to nearest shelter; SL = Standard length

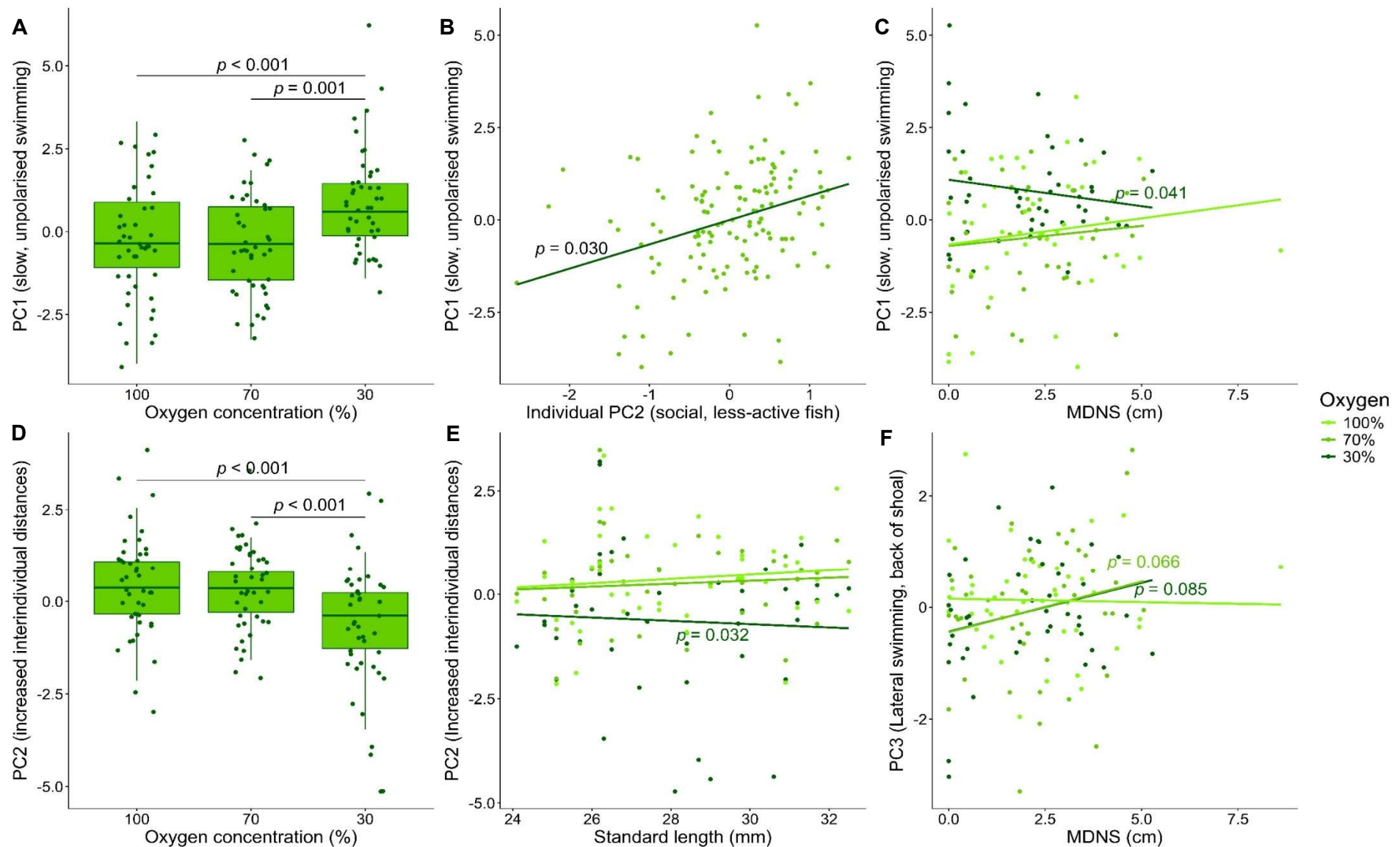


Figure 5.3A. Effects of oxygen concentration on PC1: negatively correlated with speed, positively correlated with turning angle and heading difference to nearest neighbour. **B.** Effects of individual sociability and activity level of fish on PC1. **C.** Effects of oxygen concentration on the relationship between risk-taking behaviour of individuals and PC1. **D.** Effects of oxygen concentration on PC2: positively correlated with mean distance to the centre of the shoal and nearest neighbour distance. **E.** Effects of oxygen concentration on the relationship between fish standard length and PC2. **F.** Effect of oxygen concentration on the relationship between risk-taking behaviour of individuals and PC3: positively correlated with bearing, negatively correlated with distance along group motion.

Speed of the group centroid was reduced at 30% O₂ compared with at 100% O₂ (LMM: $z = -4.134$, $p < 0.001$; Table 5.3; Figure 5.4A) and 70% O₂ (emmeans: $z = -3.999$, $p = 0.001$). Group polarisation was also reduced at 30% O₂ compared to 100% O₂ (LMM: $z = -4.887$, $p < 0.001$; Table 5.3; Figure 5.4B) and 70% O₂ (emmeans: $z = -5.032$, $p < 0.001$). There was weak evidence that group polarisation (LMM: $z = -1.738$, $p = 0.082$; Figure 5.4C) was lower in groups containing social, active individuals, regardless of oxygen level. Group speed was reduced (LMM: $z = -2.424$, $p = 0.015$) and group polarisation increased (LMM: $z = 2.596$, $p = 0.009$) with successive trials (Table 5.3). No interaction effects were retained in the group speed model ($\Delta\text{AIC} = 0.77$, Akaike weight = 0.24), however there was weak evidence for a positive effect of the interaction between MDNS and oxygen level ($\Delta\text{AIC} = 0.39$, Akaike weight = 0.15) on group polarisation at 30% O₂ (LMM: $z = 1.868$, $p = 0.062$; Figure 5.4D; Table 5.3). Groups containing individuals displaying greater risk-taking behaviour may therefore have retained greater polarisation under hypoxia.

Table 5.3. Results of linear mixed models modelling variables affecting group cohesion during group trials. Variables with evidence for an effect at $p < 0.1$ are shown in bold. * indicates significance at $p < 0.05$, ** indicates significance at $p < 0.01$, and * indicates significance at $p < 0.001$. OR = Odds Ratio. R^2 values represent pseudo- R^2 .**

Response variable	Explanatory variable	Estimate	Std. Error	z value	p	R^2_m	R^2_c
						0.082	0.679
Group speed	Intercept	1.358	0.220	6.170	<0.001***		
	High sociability, high activity (PC1)	-0.012	0.014	-0.832	0.406		
	High sociability, low activity (PC2)	-0.032	0.020	-1.562	0.118		
	MDNS (cm)	-0.009	0.010	-0.884	0.377		
	Standard length (mm)	0.002	0.007	0.244	0.808		
	70%	-0.014	0.035	-0.397	0.691		
	30%	-0.155	0.037	-4.134	<0.001***		
	Trial number	-0.042	0.017	-2.424	0.015*		
<i>Post-hoc test</i>	70-30% O₂	OR: 1.150	0.041	-3.999	0.001**		
						0.057	0.873
Group polarisation	Intercept	-0.687	0.105	-6.552	<0.001***		
	High sociability, high activity (PC1)	-0.006	0.006	-1.022	0.307		
	High sociability, low activity (PC2)	-0.014	0.008	-1.738	0.082		

	MDNS (cm)	-0.003	0.006	-0.45	0.653
	Standard length (mm)	0.001	0.003	0.284	0.776
	70%	-0.008	0.025	-0.319	0.750
	30%	-0.118	0.024	-4.887	<0.001***
	Trial number	0.018	0.007	2.596	0.009**
	MDNS*70%	-0.001	0.009	-0.102	0.919
	MDNS*30%	0.017	0.009	1.868	0.062
<i>Post-hoc test</i>	70%-30% O₂	OR: 1.070	0.015	-5.032	<0.001***
<i>Post-hoc test</i>	70-30% O ₂ *MDNS	-0.018	0.010	-1.814	0.165

MDNS = Mean distance to nearest shelter; SL = Standard length

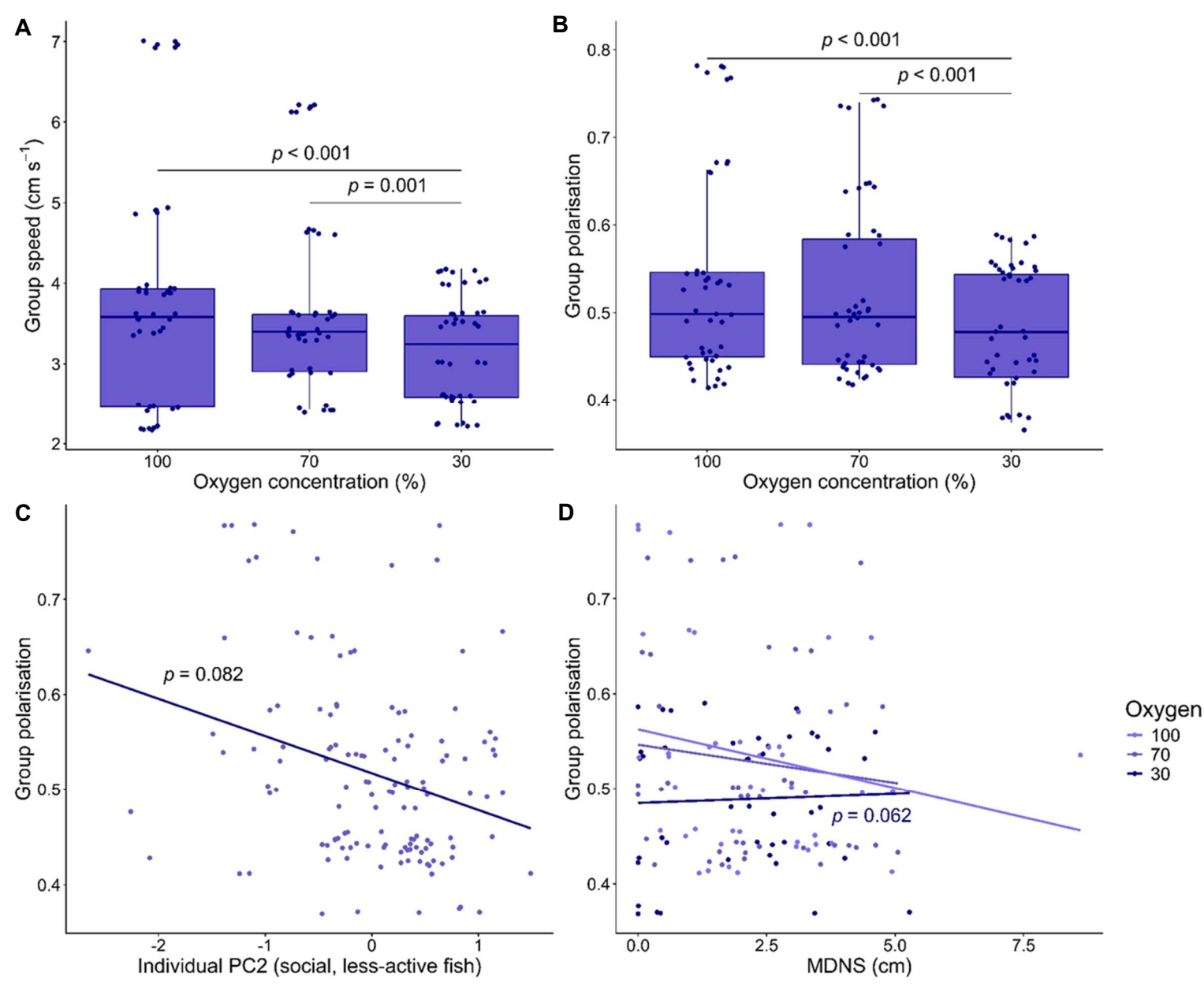


Figure 5.4. Effects of oxygen concentration on A. median speed of group centroid in group behavioural trials and B. group polarisation in group behavioural trials. C. relationship between sociability and activity traits of individuals in groups and group polarisation. D. Effect of oxygen concentration on the relationship between individual risk-taking behaviour and group polarisation.

5.5. Discussion

Hypoxia altered how individual behavioural traits related to behaviour within social groups, revealing that links between individual phenotype and collective dynamics are context dependent. Under low oxygen, fish that were less risk-averse when tested alone tended to occupy more posterior positions in shoals, while overall reductions in activity were mirrored by decreases in group speed and polarization and by changes in inter-individual spacing. These effects were strongest at 30% oxygen and weak or absent at 70%, consistent with previous work showing that pronounced behavioural disruption typically occurs only below moderate oxygen thresholds (Cook et al., 2014; Domenici et al., 2000, 2002; Killen et al., 2012; Tiddy, Munson, et al., 2024). Together, these results show that abiotic stress can reshape the translation of individual behavioural variation into group-level structure, rather than simply shifting mean behaviour, highlighting the importance of environmental context for predicting collective dynamics.

Individual activity was reduced with low oxygen availability, but hypoxia had no effect on individual sociability. Fish may reduce activity under hypoxic conditions to reduce oxygen demand, though some species increase activity in hypoxia, possibly to escape unfavourable conditions (Domenici et al., 2000; Killen et al., 2012). As freshwater fish originating from an environment where water levels vary and deoxygenation occurs frequently (Pelster & Wood, 2024; Val & de Almeida-Val, 1995), *H. rhodostomus* may favour a low-activity hypoxia coping strategy, allowing them to “wait out” hypoxic conditions. While various previous studies, including two reviews (Domenici et al., 2017; Tiddy, Munson, et al., 2024), have found effects of hypoxia on group cohesion, previous studies of the effects of hypoxia on sociability have found no evidence for an effect (Dunton et al., 2025; Sommer-Trembo et al., 2017). While it has been proposed that fish may move further from conspecifics in hypoxic conditions to reduce competition for limited oxygen (Domenici et al., 2002, 2017), this would not have been the case during our measures of sociability, as focal fish were not in competition for limited oxygen with the stimulus shoal. In the present study, however, while individuals became less active under hypoxic conditions in sociability trials, evidence for reduced activity in risk-taking behaviour trials, i.e., with no shoal visible, was weaker. Tetra may therefore reduce activity more when given visual access to conspecifics. This indicates a possible modulation of activity response depending on the social environment (Killen et al. 2026). In social fish, benefits for remaining in a shoal such as predator detection and food finding may outweigh individual physiological optima in some circumstances. In pile perch *Phanerodon vacca* individuals have been

found to sacrifice preferred swimming speed to remain with a conspecific (Tiddy et al., 2025), though this was not tested under hypoxia. Evidence for reducing activity under hypoxia to maintain group cohesion, i.e., proximity to conspecifics has been found in a related shoaling marine species, the striped surfperch *Embiotoca lateralis* (Cook et al., 2014). In Atlantic herring *Clupea harengus*, shoals with lower swimming speeds under normoxia maintained group cohesion for longer under progressive hypoxia compared to shoals with higher swimming speeds (Domenici et al., 2000). Evidence therefore exists for fish reducing swimming speed to remain with conspecifics despite physiological trade-offs including increased oxygen competition, however the factors affecting whether fish maintain sociability in individual behavioural trials require further study (Tiddy, Munson, et al., 2024).

While activity was reduced under hypoxia, R^2_c values in models for individual behavioural traits, i.e., the amount of variation explained by the full model including the random effect of individual identity, was high compared with variation explained by the fixed model effects of treatment, trial, and their interaction (R^2_m). This may indicate high behavioural repeatability across contexts in *H. rhodostomus* (Killen, Adriaenssens, et al., 2016). While repeatability was not examined in the present study due to lack of repeated measures under hypoxia, this represents an interesting avenue for further research.

Individual fish swam more slowly and were less polarised with nearest neighbours in hypoxic conditions (PC1), which corresponded to a group-level reduction in speed and polarisation. This was consistent with the reduction in activity observed in individual behavioural trials under hypoxic conditions. However, in group trials, fish moved closer together at lower oxygen levels (PC2), an effect that was exacerbated in larger fish. Previous studies have more frequently found increases in inter-individual distances, i.e., reduced group cohesion, under hypoxia (Tiddy, Munson, et al., 2024), including in seabass *Dicentrarchus labrax* (Alfonso et al., 2020), *C. harengus* (Domenici et al., 2002), Iberian barbel *Luciobarbus bocagei* (Hayes et al., 2019) and northern anchovy *Engraulis mordax* (Moss & McFarland, 1970). As discussed above, however, there is also evidence that reducing activity level may allow fish to maintain group cohesion (Cook et al., 2014; Domenici et al., 2000). In the present study the reduction in swimming speed and inter-individual distances in group trials was associated with a greater likelihood of remaining inactive in the centre of the arena, near to the shelters placed there. It is therefore possible that the observed change in inter-individual distances is more related to changes in activity

level, mediated by passive aggregation around shelters, under low oxygen than to fish choosing to remain with conspecifics despite increased competition for oxygen (Domenici et al., 2000, 2002). We did not find evidence that larger fish underwent increased reductions in activity level that could explain a greater effect of hypoxia on inter-individual distance. However, larger fish may have had slightly greater inter-individual distances under ambient conditions and “normal” activity levels due to reduced manoeuvrability (Jolles, King, et al., 2020) and higher repulsion zones (Romenskyy et al., 2017), leading to a more apparent reduction under low oxygen and low activity. While the lack of activity was also likely the main reason for the reduction in polarisation at both the individual and group levels (M. I. A. Kent et al., 2019), it has also been suggested that hypoxic conditions may reduce functioning of neural and sensory systems, such as the lateral line, in fish species (Andreassen et al., 2022; Domenici et al., 2007; Lucon-Xiccato et al., 2014; Schellart & Wubbels, 1998). Fish may therefore have found it more difficult to engage in polarised swimming under hypoxic conditions, even when group swimming did occur.

Individual behavioural traits influenced how fish were organized within groups, but these relationships were strongly context dependent. Most notably, less risk-averse individuals tended to occupy more posterior positions under hypoxia, despite also swimming faster and exhibiting stronger local alignment (Figure 5.3F). This indicates that their rearward group positioning was not a consequence of reduced locomotor capacity but instead reflects a shift in how “risky” phenotypes participate in collective movement when oxygen is limited. One explanation is that highly risk-prone fish spent more time outside cohesive shoals, joining group movement only intermittently. Then, when shoals did form, these individuals were located toward the rear. Such state-dependent expression of behavioural type is consistent with previous work showing that the relationship between individual behavioural traits and leadership can depend on social phenotype and context (Bevan et al., 2018; Herbert-Read et al., 2011; N. Miller et al., 2013). In our study, sociability did not modulate the effect of risk-taking on group structure (Jolles et al., 2017), though less-social, more active individuals swam faster and were more polarised with nearest neighbours regardless of oxygen concentration (Figure 5.3B), and there was weak evidence that individual sociability and activity also affected polarisation at the group level (Figure 5.4C). Together, these results suggest that hypoxia and group phenotypic composition have both independent and interactive effects on collective dynamics, and that behavioural traits measured in isolation do not translate into fixed spatial or functional roles within groups.

An effect of trial number was found on various behaviours measured in group trials, consistent with previous work showing reduced social tendencies and collective behaviour in fish shoals with repeated testing (MacGregor & Ioannou, 2021). However, as treatment order was reversed in half of group trials, this temporal effect does not prevent detection of the effects of hypoxia from our models. As changing of oxygen availability was carried out consistently from high to low in individual trials, temporal control trial data was used in models to separate effects of hypoxia from those of time or repeated exposure.

5.6. Conclusions

As hypoxic events become more common in aquatic systems, predicting behavioural responses requires understanding not only how individuals are affected, but how these changes influence social interactions and collective dynamics. Behavioural adaptations are often considered to be among the first lines of defence in coping with or avoiding unfavourable conditions, and social behaviour is a key adaptive trait in gregarious fish species. We show that reduced oxygen availability alters both the structure of shoals and the functional roles that different behavioural phenotypes occupy within them, demonstrating that the translation of individual traits into social function is environmentally dependent. Hypoxia therefore has the potential to reorganize social behaviour in gregarious fish, rather than simply altering individual activity. By linking individual variation to group-level outcomes across environmental conditions, our results highlight the need to incorporate social context into forecasts of how fish populations will respond to ongoing environmental change.

Chapter 6

Effects of artificial light at night on the diurnal risk-taking behaviour of a gregarious reef fish

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6.1. Abstract

Artificial light at night (ALAN) is increasingly prevalent in both terrestrial and aquatic systems and influences physiological and behavioural traits of wild animals across a range of habitats. In coral reef ecosystems, increasing human pressure contributes to an increase in ALAN exposure for reef organisms. In the present study, we investigated the effects of chronic exposure to ALAN in the wild on diurnal risk-taking and social behaviour in a gregarious coral reef fish, *Dascyllus trimaculatus*. Fish were collected from sites exposed to ALAN or control light levels and underwent an emergence test to assess diurnal risk-taking behaviour and a 3-chamber shoal choice test to assess sociability. Activity levels were measured during both tests. ALAN-exposed fish took less time to emerge from an anemone compared with control fish. We found evidence for reduced activity in ALAN-exposed fish in sociability trials. Increased risk-taking may be due to either direct effects of ALAN exposure or selective mortality of more risk-averse individuals in the wild due to an increased risk of starvation or reduced growth. While we did not find evidence for increased diurnal activity, ALAN exposure may lead to increasing metabolic needs, driving

increased risk-taking and foraging, or selective mortality. However, the increased risk-taking behaviour of ALAN-exposed fish did not increase distance to a conspecific shoal, i.e. no effect on sociability. Our study provides evidence that chronic ALAN exposure in the wild increases risk-taking behaviour in a marine fish.

6.2. Introduction

Anthropogenic stressors are increasingly common throughout natural systems. Stressors such as light pollution cause significant threats to wildlife through disruption of the neuroendocrine stress axis and natural rhythms (Gaston & Sánchez de Miguel, 2022; Marangoni et al., 2022). A growing number of rural areas are experiencing light pollution from both temporary and permanent light sources, with global light emissions having increased by close to 50% since 1972 (Sánchez de Miguel et al., 2021). As human settlements become more widespread, coastal infrastructure and activities bring artificial light to aquatic as well as terrestrial habitats (Sanders et al., 2020), with an estimated 22% of coastlines exposed as of 2010 (Davies et al., 2014), a figure that has likely since increased (Sánchez de Miguel et al., 2021). The effects of these stressors on animal physiology and behaviour in coastal and aquatic systems in particular are therefore of increasing research interest (Marangoni et al., 2022; Tiddy, Cortese, et al., 2024).

Artificial light can frequently have sub-lethal effects that influence individual fitness or even entire ecosystems (Gaston & Sánchez de Miguel, 2022; Underwood et al., 2017). In particular, nocturnal light pollution, often referred to as artificial light at night (ALAN), can have a range of physiological and behavioural effects on wild animals. For example, ALAN disrupts natural cycles of melatonin production (Gaston & Sánchez de Miguel, 2022; Grubisic et al., 2019), a hormone essential for regulating circadian rhythms and sleep. This disruption can have detrimental effects, including impaired immune function and increased oxidative stress (Zhao et al., 2019). Organisms can also become more active because of disruption to sleep cycles (Georgiou et al., 2024; Pulgar et al., 2019), which if not compensated by increased food intake, may decrease the energy available for growth and reproduction. Chronic ALAN exposure, defined as lasting >10% of an organism's lifespan (Suter, 2016), has been found to reduce growth and survival in a marine fish species (Schligler et al., 2021), while acute ALAN exposure has been found to affect fish embryo quality but not larval morphology or swimming performance in a coral reef fish (Roost et al., 2025). Acute ALAN also reduces nestling growth in birds (Raap et al., 2016). Changes to growth rate may affect reproductive success, through delays in sexual maturity

and altered resource allocation for reproduction (Leclercq et al., 2011). In the marine environment, acute ALAN was found to increase adult growth rate but reduce larval swimming capacity and escape responsiveness in offspring of a reef fish (Schligler, Roost, et al., 2026). Animals may also be attracted to or repelled by light, thus altering space use within the environment (Keep et al., 2021; McLeod & Costello, 2017) and changing nighttime communities (Weschke et al., 2024). Detection of visual or non-visual cues may be altered, as organisms that ordinarily rely on other sensory apparatus at night may make more use of vision under ALAN conditions (Chaput et al., 2023). ALAN exposure in the embryonic phase may also impair cognitive functions such as learning in larvae post-hatching, as observed in zebrafish *Danio rerio* (Lucon-Xiccato et al., 2023). Effects of ALAN on fitness-related behaviours such as social and foraging behaviour have been found in a variety of organisms such as birds, bats, and invertebrates (Kempnaers et al., 2010; Kurvers & Holker, 2015; Ryer & Olla, 1998). However, the impacts of ALAN on social behaviour in aquatic organisms, particularly fishes (Tiddy, Cortese, et al., 2024), remain understudied.

A key adaptive behaviour in many species is social behaviour, in the form of living and travelling in groups (Killen, Marras, et al., 2017; Pitcher, 1983). Benefits of group living may include increased foraging success, predator avoidance, and mate choice (Pitcher et al., 1982; A. Ward & Webster, 2016b, 2016a). Various forms of anthropogenic stressors affect social behaviour in animals, such as hypoxia and various chemical pollutants (Michelangeli et al., 2022; Tiddy, Cortese, et al., 2024; Tiddy, Munson, et al., 2024). The effects of light pollution on social behaviour in animals are relatively understudied, despite existing evidence of effects of ALAN on physiology and alterations in behaviours such as risk-taking and activity levels (Kurvers et al., 2018; Pulgar et al., 2019). Changes in sociability may be influenced by risk-taking, as higher risk-taking may be linked to a tendency to stray further from conspecifics (Conrad et al., 2011; Harcourt et al., 2009; Pike et al., 2008). In addition, vision is a key component of coordinating group behaviour (Chaput et al., 2023). ALAN exposure may therefore affect the interplay between physiological changes and behaviour (Pulgar et al., 2019), potentially leading to lasting effects such as changes in diurnal activity or social behaviour impacted by changes in risk-taking. Among terrestrial species, reduced risk-taking behaviour in response to ALAN has been found in an isopod species (Dissegna & Chiandetti, 2025). In the aquatic environment, freshwater guppies *Poecilia reticulata* showed no changes in diurnal sociability after 10 wk of light exposure in the lab, but exhibited increased diurnal risk-taking behaviour (Kurvers et al.,

2018). In contrast, a study on a marine species, *Dascyllus aruanus*, found no effect on risk-taking behaviour in wild fish following short-term (2 wk) exposure to ALAN but did find increased nocturnal activity (Georgiou et al., 2024). Evidence for behavioural effects of ALAN in fish is therefore mixed, and more research is needed to elucidate the impacts of this increasingly common stressor.

Despite the evidence for physiological and behavioural changes resulting from short-term ALAN exposure (Georgiou et al., 2024; Kurvers et al., 2018), the effects of chronic exposure to ALAN on social behaviour in wild populations of gregarious fish species are largely unknown. In the present study, we aim to add to this body of knowledge by conducting the first study on the effects of chronic exposure to ALAN in the wild on diurnal social and risk-taking (emergence) behaviours in fishes. We used emergence from a shelter following a startle (chase) stimulus as a proxy for risk-taking (Beckmann & Biro, 2013), as emergence from a shelter puts fish at greater risk of predation (Kurvers et al., 2018). The use of emergence behaviour as a proxy for risk-taking has been established in several species, including damselfish (Beckmann & Biro, 2013; Harris et al., 2010). We used distance to a stimulus shoal as a proxy for sociability, and percentage time spent moving in both tests to measure activity levels in a marine fish, threespot dascyllus *Dascyllus trimaculatus*. This species was selected for its highly gregarious nature, as individuals typically form shoals closely associated with anemones. They are also site-attached as juveniles and adults (Hayashi et al., 2020; Schmitt & Holbrook, 1996), and thus it is possible to derive the environmental conditions to which they have been exposed based on sites where they are found. We focused on diurnal behaviours, as this allowed us to examine the carry-over effects of prior ALAN exposure on daytime responses to a simulated predator chase, exposure to a conspecific shoal, and activity level. Coral reef fishes such as *D. trimaculatus* are increasingly exposed to ALAN as coastal and offshore infrastructure expansion leads to greater levels of anthropogenic stressors in their habitats (Aubrecht et al., 2008; Davies et al., 2016). We predicted that risk-taking behaviour would be higher in ALAN-exposed fish and that ALAN exposure would also be associated with a reduction in social behaviour and increase in diurnal activity level in *D. trimaculatus* (Conrad et al., 2011; Harcourt et al., 2009; Pike et al., 2008).

6.3. Materials and Methods

6.3.1. Study animals

A total of 24 juvenile *Dascyllus trimaculatus* were collected from 3 subtidal fringing reef locations along the shores of Mo'orea, French Polynesia (Figure 6.1A). Juvenile *D. trimaculatus* were used as these were more common, and comparing among life stages adds an additional source of variation. In addition, juvenile *D. trimaculatus* have greater site fidelity than adults, allowing more certainty in their degree of wild ALAN exposure. Seven months prior, 30 wild, empty anemones *Radianthus magnifica* approximately 30–40 cm in diameter were collected from the north-western lagoon of Mo'orea where they are highly abundant but rarely host fish. Anemones were then transplanted to our sites by S.C.M. and Thibaut Roost as described in Schligler et al. (2021). Anemones were placed at sites with varying light levels: 15 at naturally lit sites (control) and 15 at sites exposed to chronic terrestrial lighting from nearby hotels (ALAN). Light exposure on sites was in the form of direct LED spot lighting placed above the water. These were present at the hotels on pontoons and were not experimentally supplemented (Figure 6.1B). Fish used in testing were all collected from different anemones. The 3 locations were situated either on the north shore (Site 1: 17°29'01.9"S, 149°50'37.8"W; $n = 14$ fish and Site 2: 17°28'47.6"S, 149°48'13.8"W; $n = 2$ fish; Figure 6.1A) or on the east shore of Mo'orea (Site 3: 17°30'05.3"S, 149°45'51.1"W; $n = 8$ fish). Control and ALAN sites were situated 50–200 m apart on comparable fringing reefs, ensuring that fish experienced similar environmental conditions, except nighttime light exposure. *D. trimaculatus* settle into anemones after their pelagic larval phase, and are site-attached—meaning that individuals remain in the same anemone after settlement—and had thus been exposed to treatment light levels (either control or ALAN) each night since settlement.

Light levels at each site were measured overnight using light loggers placed on the reef at the level of anemones, taking 1 measure min^{-1} from 18:00–06:00 h. A minimum of 1 and a maximum of 8 overnight measurements were taken per treatment per site, all within 8 d of the full moon (Supplementary Table 6.1). Nocturnal light levels (18:00–06:00 h) under control conditions were consistently <0.01 lx across sites (mean $\pm$ SE: Site 1 = 0.006 ± 0.001 lx, number of overnight samples = 3; Site 2 = 0.002 ± 0.0009 lx, $n = 2$; Site 3 = 0.008 ± 0.002 lx, $n = 2$; Figure 6.1C). Under ALAN, mean light levels were 10.4 ± 0.14 lx at Site 1 ($n = 8$), 4.27 ± 0.06 lx at Site 2 ($n = 7$), and 21.2 ± 0.71 lx at Site 3 ($n = 1$) (Figs. 1B & S1, Supplementary Table 6.1), though only fish from anemones exposed to control

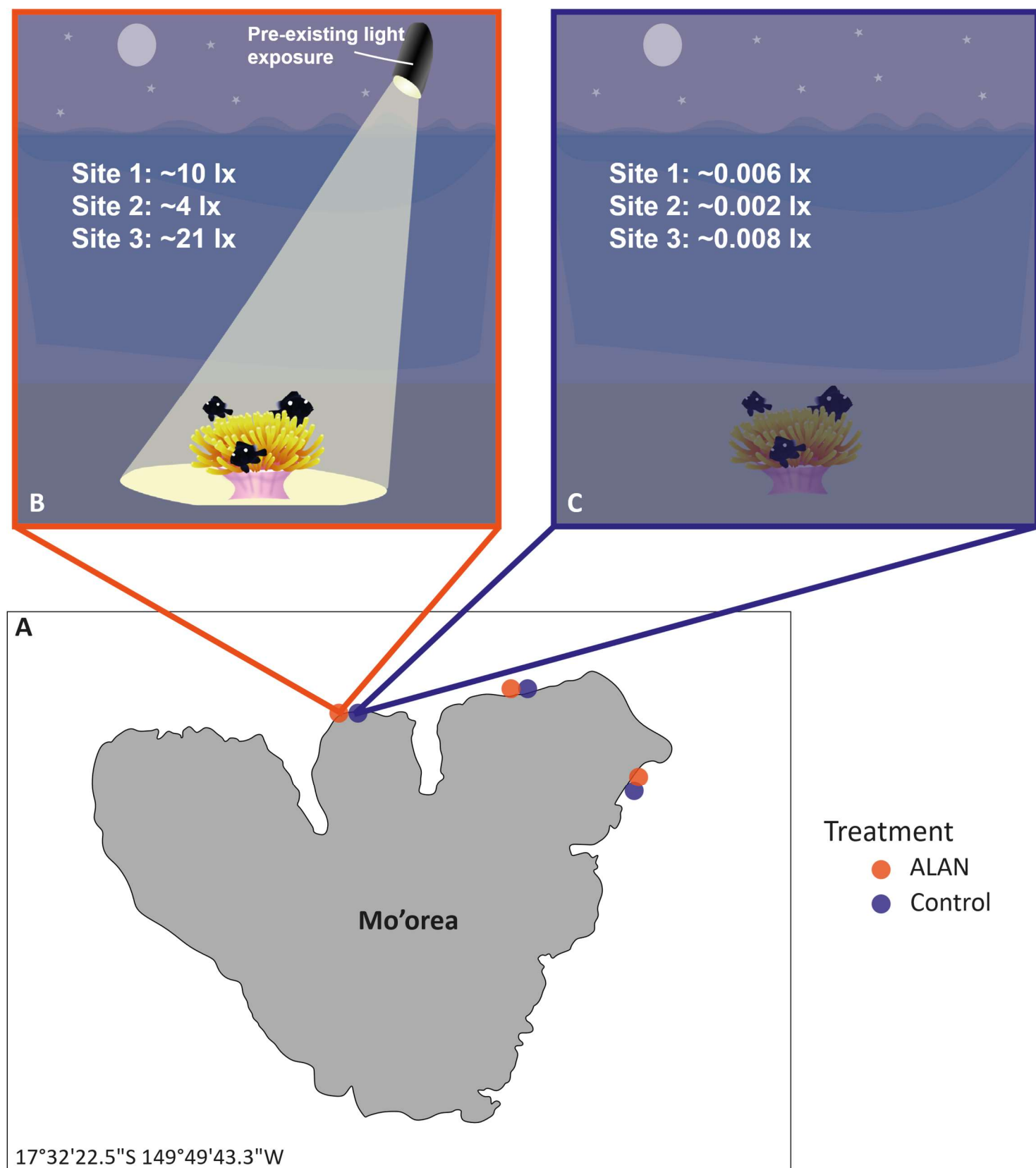


Figure 6.1A. Map showing site locations in Mo'orea, French Polynesia, and diagram showing B. ALAN and C. control treatment conditions. Light levels indicate readings taken under control and ALAN conditions within eight days of the full moon.

light levels were collected from Site 2. The lagoon around Mo'orea does not experience tides, so water levels are consistent throughout the month.

Following collection, fish were brought to CRIOBE research station. Due to logistical constraints, they were grouped according to light exposure treatment and site in the wild but not according to their original anemone or individual light exposure history. As a result, individual variation in light exposure experienced in the wild could not be accounted for in the model. All fish were held for a minimum of 72 h prior to testing to allow acclimation to the lab environment and to reduce any effects of stress from transportation. All but 2 fish were captured between 3 and 5 d prior to behavioural testing. Two fish from Site 2 were held in the lab for longer (15 d) due to logistical constraints. Fish were fed twice daily, and tanks were constantly refreshed with seawater, maintaining temperature at ambient levels. Control fish were held under 'natural' light conditions (12 h light:12 h dark). ALAN fish were held under the same daylight conditions (12 h) as the control fish but at night (12 h) were exposed to light levels of 6.4 lx. Light levels in the lab were slightly lower than in the field to avoid exposing control fish to artificial light during holding, as tanks were in the same area due to limited holding space. ALAN in the lab was produced using above-water standing LED tube lights placed between tanks. Lights were stood between tanks rather than being suspended from the ceiling to allow light exposure to be confined to tanks containing ALAN fish; this was achieved by placing screens around ALAN tanks to prevent control tanks from being exposed. Fish age varied, due to limited numbers of fish available at sites; however, all fish were juveniles as seen by the presence of white spots on the body and head and fish lengths (Raharinaivo et al., 2020). Fish were not sexed. A total of 12 control and 12 ALAN-exposed fish were used in trials.

6.3.2. *Sociability testing*

Behavioural testing arenas consisted of 3 chambers separated by transparent Perspex (Nunes et al., 2017) (Supplementary Figure 6.2A). All chambers were filled to a depth of approximately 14 cm with seawater freshly pumped from the lagoon. Prior to behavioural testing, anemones of similar size were placed in each of the side chambers. One of the side chambers contained a stimulus shoal consisting of fish collected from control conditions, which were not used in behavioural testing. The side on which the stimulus shoal was placed was alternated between trials. Stimulus shoal size was initially 5 fish; however, due to logistical reasons after 8 trials, this had to be reduced to 3 fish for the remaining 16 trials. Focal fish were placed within a transparent cylinder in the centre of the central

chamber without an anemone and allowed to acclimate for 5 min. Following this, the cylinder was removed, and fish were allowed to roam freely around the arena. Fish were filmed from above for 10 min following release, using a GoPro Hero 12 camera on linear mode in 4K, with a frame rate of 30 fps.

Sociability test videos were processed using the movement tracking software EthoVision (Version 15) (Noldus et al., 2001). Two variables were collected from each test, measured at a rate of 1 data point per frame (30 data points s⁻¹). These were percentage time spent moving (activity level), and sociability, measured as mean distance to the compartment containing the stimulus shoal (DCS) (Table 6.1, Supplementary Figure 6.2A). Percentage time spent moving was calculated as the proportion of the trial that fish spent moving at or above 1 cm s⁻¹. This threshold was determined based on the distribution of velocity values indicating that movement speeds below 1 cm s⁻¹ were likely due to small shifts in position or tracking glitches rather than swimming.

Table 6.1. Metrics measured in emergence and sociability trials

Behavioural metric	Measurement method	Ecological significance
Risk avoidance	Tendency to hide in shelter following chasing	Changes in tendency to use a shelter may affect predation risk
Emergence (risk-taking behaviour)	Tendency to emerge from shelter	Changes in tendency to emerge and time to emerge from a shelter may affect predation risk and foraging success, and affect metabolic rate through changes to activity level Maintaining proximity to a shelter may reduce predation risk but also reduce foraging opportunities
	Time to emerge from shelter	
	Mean distance to shelter after chase stimulus	
Sociability	Mean distance to conspecific shoal	Proximity to and time spent with a conspecific shoal has effects on foraging success, predator avoidance, mate finding, and may lead to metabolic changes e.g. due to “calming” effects of conspecifics in social species
Activity level	Percentage time spent moving	Time spent moving is directly related to metabolic costs but also may relate to social group cohesion and foraging success

6.3.3. Risk-taking behaviour

Testing of risk-taking behaviour was conducted immediately after sociability testing, with stimulus shoals remaining visible to the focal fish (Supplementary Figure 6.2B). Stimulus shoals were not removed or hidden from the focal fish because, as a social species, *D. trimaculatus* are unlikely to experience threats in isolation, and therefore measuring emergence behaviour with conspecifics present is a more ecologically relevant scenario. An anemone was placed in the centre of the central chamber. As various anemones ($n = 5$) were used in different trials, anemone ID was recorded for inclusion in models. Immediately following the introduction of the anemone, fish were chased by hand for 1 min. A shorter startle stimulus such as described in Beckmann & Biro (2013) was initially attempted but did not cause fish to hide, meaning a longer ‘chase’ stimulus was used instead. Fish were chased to the intensity required to elicit constant movement, i.e., a constant stress escape response, until fish hid in the anemone. If fish hid in the anemone before 1 min had elapsed, the ‘chaser’ continued to disturb the water and discourage the fish from leaving the anemone until 1 min had passed. Fish therefore received a similar stimulus regardless of when or if they hid in the anemone. If fish did not hide after 1 min, chasing was ceased, and the absence of hiding was noted. Fish were then filmed from above for 10 min, using a GoPro Hero 12 camera. Of the 24 trials, 3 were unsuccessful (2 ALAN and 1 control), 1 due to fish mortality (cause unknown) and 2 due to camera malfunctions. The final sample size was therefore ALAN $n = 10$ and control $n = 11$. The focal fish was then removed and weighed (g) and measured (total length in cm).

Six variables were recorded from each emergence test: whether fish hid in anemones (yes/no), whether fish emerged from anemones (yes/no), time until emergence in seconds, mean distance to anemone after the chase stimulus, percentage time spent moving after the chase stimulus, and distance to the conspecific shoal after the chase stimulus (Table 6.1). Behavioural measures were extracted using EthoVision. Emergence was defined as the entire fish, including the tail, emerging from the anemone for at least 1 s. Where fish did not emerge, time to emergence was recorded as 600 s. Most fish ($n = 14$) hid within the anemone after 1 min of chasing, but when fish did not hide (control $n = 4$, ALAN $n = 3$), time to emergence was recorded as 0 s. Variables measured after the chase stimulus were only measured when fish were outside the anemone, i.e. were not measured for fish that hid in anemones and did not emerge within 10 min.

6.3.4. Statistical analysis

Data were analysed in R version 4.5.2 (R Core Team, 2025) using the generalized linear mixed modelling (GLMM) package glmmTMB (Brooks et al., 2017). Due to the variance in body size among individuals used in trials, Welch's t tests were used prior to modelling to test for potentially confounding differences in size (mass or length) between treatment groups.

For sociability trials, 2 linear mixed models (LMMs) were constructed, with response variables of mean distance to the conspecific shoal in cm (social behaviour in sociability trials; hereafter sociability_s) and percentage time spent moving (activity in sociability trials; hereafter activity_s). Sociability_s was natural log transformed to meet model assumptions. Two additional LMMs were constructed to check for any effect of stimulus shoal size or placement on sociability variables. The response variables for these models were sociability_s and activity_s, while the explanatory variables were stimulus shoal size, stimulus shoal side, and treatment (control or ALAN). Collection site as a factor (1, 2, or 3) was also included as a random effect in all LMMs.

For emergence trials, 4 models were constructed corresponding to the 4 continuous emergence variables. For time until emergence, only fish that hid were included in the model ($n = 14$). Fish that did not emerge from anemones were excluded from the data for the other emergence variables (post-chase stimulus behaviour); however, fish that did not hide were included. Mean distance to the anemone (cm), percentage time spent moving (activity in emergence trials; hereafter activity_e), and mean distance to the conspecific shoal (cm) (sociability in emergence trials; hereafter sociability_e) were calculated only including data from the point of initial emergence so that data would not be skewed towards zero for fish that spent a greater amount of time in the anemone. LMMs were constructed for sociability_e and time to emerge, while a beta-distributed GLMM was used for activity_e due to violation of model assumptions for LMMs, which could not be normalized by transformation. Time to emerge was natural log transformed to meet model assumptions. For mean distance to the anemone, while data from prior to initial emergence was excluded, some fish returned to the anemone or remained close to it. This led to a high number of very low values, therefore a zero-inflated beta-distributed GLMM was used, with values of <1 cm distance of the fish centroid from the anemone taken as zero values. Mean distance to the anemone was transformed according to Eq. (S6.1) in the Supplement to meet the distribution required by zero-inflated beta ($0 \leq y < 1$) models. For the 2

categorical variables, Fisher's exact test was performed on frequency count data for each treatment, i.e. the number of fish that hid/did not hide for ALAN and control treatments and the number of fish that emerged/did not emerge for ALAN and control treatments. Fisher's exact test was used over a GLMM with a binomial distribution, as the lack of variation within the ALAN group for whether fish emerged (all fish emerged) resulted in highly skewed standard error estimates in the GLMM output (estimate = 40.5 ± 25360000).

GLMMs and LMMs contained 2 fixed explanatory variables. These were treatment (ALAN or control) and body mass of the focal fish (g). In each model, location (site) from which fish were caught and holding time in the lab for each individual were included as random effect variables. In sociability models, number of fish in the stimulus shoal was included as a random effect variable. In emergence models, ID of the anemone placed in the central chamber was included as a random effect variable. Two additional LMMs were constructed to examine whether sociability and activity differed between sociability and emergence trials, i.e., before and after the chase stimulus. The response variables for these models were natural log-transformed sociability and percentage time spent moving, respectively, while the explanatory variables were treatment, body mass, and trial type (sociability or emergence). Fish ID nested with in capture site was included as a random effect variable. Holding time in the lab was also included as a random effect. Sociability and activity were modelled separately for sociability trials, emergence trials, and the comparison between these due to our limited sample size meaning statistical power would not be sufficient to include multiple interactions in one large model. Model assumptions for all models were tested using the 'simulateResiduals' function in the model diagnostics package DHARMa (Hartig, 2016). Specifically, models were tested for observed vs. predicted residual distribution (KS test), dispersion (homogeneity), and outliers. Some variables were transformed as described above where necessary to meet model assumptions. Data were plotted using the ggplot2 (Wickham, 2016) and ggmap (Kahle & Wickham, 2013)(Kahle & Wickham, 2013) packages.

As originally recommended by Fisher (1922), we use *p* values as a continuous indicator of the strength of evidence for the alternative hypothesis and discuss results according to the language suggested in Muff et al. (2022).

6.4. Results

6.4.1. Study animals

Fish collected ranged in length and weight from 1.6–9.6 cm and 0.23–19.7 g, with means ($\pm$ SE) of 4.4 ± 0.64 cm and 5.38 ± 1.79 g from ALAN and 4.9 ± 0.33 cm and 4.79 ± 0.85 g from control sites. Exposure duration in the field therefore varied, as larger and thus older fish would have been exposed to their respective light conditions for a longer period. However, since there was no significant difference in length or weight between light treatments (Welch's t test: $p > 0.1$; Supplementary Table 6.2), the exposure duration was unlikely to differ significantly. Neither stimulus shoal size nor the side on which the stimulus shoal was placed had any effect on sociability_s (Supplementary Table 6.3).

6.4.2. Sociability test

Of the 24 fish included in the analysis, 23 spent most of their time closer to the chamber with the conspecific shoal than to the empty chamber. ALAN treatment did not influence sociability_s (mean distance to a conspecific shoal; Table 6.2); however, there was reduced activity_s in ALAN-treated fish (percentage time spent moving; LMM: $z = -1.994$, $p = 0.046$; Figure 6.2A, Table 6.2). Greater mass of the fish was associated with reduced sociability_s (increased DCS; LMM: $z = 3.188$, $p = 0.001$; Figure 6.2B, Table 6.2) and increased activity_s (LMM: $z = 2.243$, $p = 0.025$; Figure 6.2C, Table 6.2). Behavioural trait data distributions for individual fish can be found in Supplementary Figures 6.3A, B.

6.4.1. Emergence test

Of 21 successful emergence tests, 7 fish (3 ALAN and 4 control) did not hide in anemones after 1 min of chasing. ALAN exposure did not affect whether fish hid in anemones after chasing (Fisher's exact test: $p = 1$, upper 95% CI = 6.521, lower 95% CI = 0.079). Neither distance from anemone nor activity_e were correlated with mass or ALAN exposure (Table 6.3). Among fish that did hide, there was strong evidence that control fish took longer to emerge from the anemone as compared to those that had been exposed to ALAN (LMM: $z = -4.689$, $p < 0.001$; Table 6.3, Figure 6.2D). We found moderate evidence that larger fish also emerged more quickly from anemones following a chase stimulus (LMM: $z = -2.501$, $p = 0.012$; Table 6.3, Supplementary Figure 6.4). There was weak evidence that fish exposed to ALAN were more likely to emerge from anemones within 10 min (Fisher's exact test: $p = 0.07$, upper 95% CI = 1.177, lower 95% CI = 0; Figure 6.2E). Treatment had no effect on sociability_e after the chase stimulus, but there was weak evidence for an effect of body mass, with larger fish possibly being closer to the conspecific shoal in emergence

trials (LMM: $z = -1.923$, $p = 0.055$; Figure 6.2B, Table 6.3). Sociability (LMM: $z = -6.096$, $p < 0.001$; Figure 6.2B, Table 6.4) and activity (LMM: $z = 2.101$, $p = 0.036$; Figure 6.2A; Table 6.4) were significantly reduced after the chase stimulus (emergence trial) compared with before (sociability trial), regardless of treatment.

Table 6.2. Results of LMMs analysing behaviour of *Dascyllus trimaculatus* in sociability trials. ALAN treatment was analysed relative to fish exposed to control light levels. * indicates significance at $p < 0.05$; ** indicates significance at $p < 0.01$; * indicates significance at $p < 0.001$. Variables with evidence for significant effects at $p < 0.1$ are shown in bold.**

<i>Model response variable</i>	Variable	Estimate	Standard error	z value	p value
<i>Distance to a conspecific shoal</i>					
	Intercept	1.424	0.434	3.283	0.001
	Treatment (ALAN)	0.170	0.194	0.876	0.381
	Mass (g)	0.062	0.019	3.188	0.001**
<i>Percentage time spent moving</i>					
	Intercept	0.672	0.070	9.613	< 0.001
	Treatment (ALAN)	-0.112	0.056	-1.994	0.046*
	Mass (g)	0.012	0.005	2.243	0.025*

Activity was also greater in larger fish in the comparison model (LMM: $z = 2.335$, $p = 0.020$; Table 6.4). Behavioural distributions for individual fish can be found in Supplementary Figures 3C–E. Correlations among traits in sociability and emergence trials are shown in Supplementary Table 6.4 and Supplementary Figure 6.5.

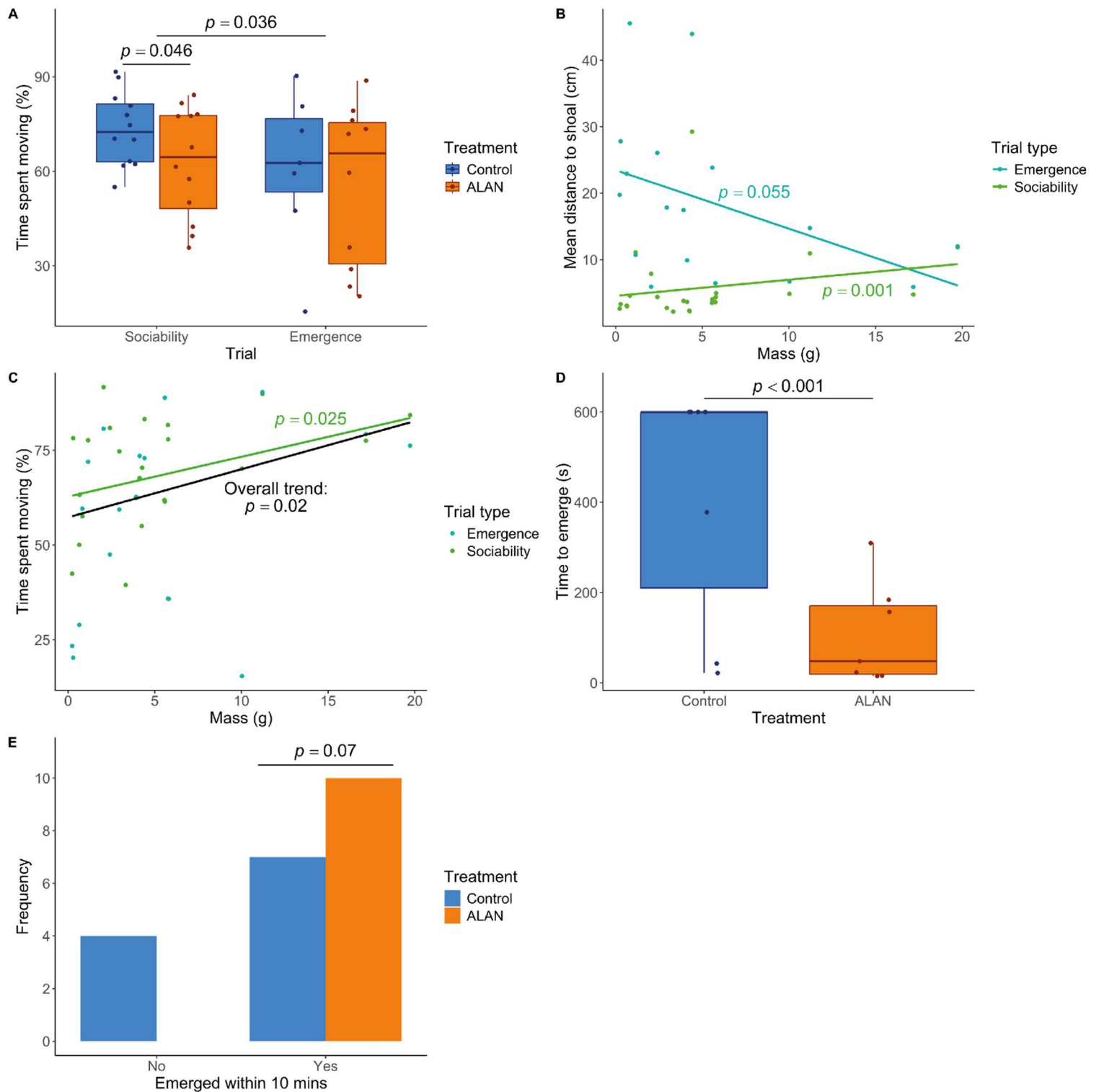


Figure 6.2A. Percentage time spent moving (activity) in *Dascyllus trimaculatus* before (sociability) and after (emergence) the chase stimulus, according to light treatment. **B.** Mean distance of the focal fish to the conspecific shoal before (sociability) and after (emergence) the chase stimulus, according to fish mass. **C.** Time spent moving before (sociability) and after (emergence) chase stimulus, according to fish mass – overall trend (black line) represents analysis on data from both trials. **D.** Time taken for fish that hid in anemones to emerge. **E.** Number of fish emerging from anemones within 10 min, grouped by treatment. Box plots show median (horizontal line), first and third quartiles (box), 1.5 times the interquartile range (whiskers), and individual data points (dots).

Table 6.3. Results of (G)LMMs analysing behaviour of *Dascyllus trimaculatus* in emergence trials i.e., following a chase stimulus. ALAN treatment was analysed relative to fish exposed to control light levels. * indicates significance at $p < 0.05$; ** indicates significance at $p < 0.01$; * indicates significance at $p < 0.001$ ***. Variables with evidence for significant effects at $p < 0.1$ are shown in bold.**

<i>Model response variable</i>	Variable	Estimate	Standard error	z value	<i>p</i> value
<i>Mean distance to shelter - conditional model</i>					
	Intercept	0.466	0.727	0.641	0.521
	Treatment (ALAN)	0.190	0.655	0.290	0.772
	Mass (g)	-0.052	0.059	-0.894	0.371
<i>Mean distance to shelter - zero-inflated model</i>					
	Intercept	0.041	1.162	0.035	0.972
	Treatment (ALAN)	-0.135	1.187	-0.114	0.909
	Mass (g)	-0.202	0.185	-1.094	0.274
<i>Distance to a conspecific shoal</i>					
	Intercept	23.57	4.681	5.036	< 0.001
	Treatment (ALAN)	0.056	5.237	0.011	0.991
	Mass (g)	-0.876	0.455	-1.923	0.055
<i>Percentage time spent moving</i>					
	Intercept	0.121	0.381	0.316	0.752
	Treatment (ALAN)	-0.224	0.427	-0.525	0.600
	Mass (g)	0.058	0.039	1.517	0.129
<i>Time to emerge from shelter</i>					
	Intercept	5.778	0.645	8.964	< 0.001
	Treatment (ALAN)	-1.826	0.389	-4.689	< 0.001***
	Mass (g)	-0.122	0.049	-2.501	0.012*

Table 6.4. Results of LMMs comparing behaviour in sociability tests and in emergence tests i.e., before and after a chase stimulus. ALAN treatment was analysed relative to fish exposed to control light conditions. The reference level for trial type is emergence. * indicates significance at $p < 0.05$; ** indicates significance at $p < 0.01$; * indicates significance at $p < 0.001$ ***. Variables with evidence for significant effects at $p < 0.1$ are shown in bold.**

<i>Model response variable</i>	Variable	Estimate	Standard error	z value	p value
<i>Distance to a conspecific shoal</i>					
	Intercept	2.765	0.223	12.39	< 0.001
	Trial type (Sociability)	-1.122	0.199	-6.096	< 0.001***
	Treatment (ALAN)	-0.055	0.202	-0.273	0.785
	Mass (g)	-0.002	0.019	-0.112	0.911
<i>Percentage time spent moving</i>					
	Intercept	0.550	0.063	8.765	< 0.001
	Trial type (Sociability)	0.108	0.051	2.101	0.036*
	Treatment (ALAN)	-0.092	0.060	-1.541	0.123
	Mass (g)	0.014	0.006	2.335	0.020*

6.5. Discussion

We found that diurnal risk-taking behaviour, specifically time to emerge from a shelter, in *Dascyllus trimaculatus* was greater in fish previously exposed to chronic ALAN in the wild. The observed increase in risk-taking indicates that physiological effects of ALAN exposure, such as changes to circadian rhythms and energy budgets (Gaston & Sánchez de Miguel, 2022; Schligler et al., 2021), are likely to translate into effects on behaviour. In contrast, we found no difference in sociability between treatments. We did, however, find an effect of fish size on sociability, indicating that larger fish were less social regardless of exposure to ALAN. Contrary to our expectation, we also found that ALAN fish showed reduced activity in sociability trials. This study is the first to investigate the effects of chronic exposure to ALAN in the wild on sociability in fish, contributing new insights to the growing body of evidence regarding the impact of non-chemical pollutants on animal social behaviour. Our study builds on the findings of Kurvers et al. (2018), which is the only prior study on the effects of ALAN on sociability in fishes. As these effects may translate to intra- and interspecific and even ecosystem level effects (Gaston & Sánchez de Miguel, 2022; Underwood et al., 2017), more work is needed to investigate the effects of ALAN on social behaviour.

Our results suggest that emergence from hiding after a chase stimulus happened sooner in *D. trimaculatus* previously exposed to ALAN, indicating an increase in risk-associated behaviour. Our findings are consistent with previous work in a freshwater fish by Kurvers et al. (2018), which found that guppies exposed to ALAN for 10 wk in the lab and tested under daylight conditions emerged sooner from a refuge compared with fish exposed to dark nights. This suggests that ALAN may shift behavioural trade-offs toward bolder strategies, potentially by altering circadian rhythms, energetic demands, or predator detection. Kurvers et al. (2018) speculated that increased nocturnal activity caused by ALAN exposure may increase metabolic needs and thus risk-taking behaviour associated with foraging. Increased nocturnal activity has been previously found in *D. aruanus* exposed to ALAN (Georgiou et al., 2024), though that study did not find any effect on risk-taking behaviour. While we did not measure nighttime activity, we did observe reduced diurnal activity levels prior to a chase stimulus in ALAN-exposed fish. This may function to conserve energy or because foraging and other movement-related needs have been partially met during nocturnal activity (Latchem et al., 2021). Pulgar et al. (2019) reported that intertidal baunco *Girella laevis* exposed to ALAN showed increased overall activity over 24 h, but their activity cycles were altered, with reduced afternoon activity compared to controls. The effects of ALAN on activity level may therefore be dependent on both species and time of day, and further study is needed to elucidate any links between activity level, metabolic demands, and changes to other behaviours such as sociability and risk-taking.

Another explanation put forth by Kurvers et al. (2018) is that ALAN increases risk-taking similarly to how animals in ‘stressful’ high predation environments often show elevated risk-taking behaviour (Harris et al., 2010). Light exposure may act as a stressor, eliciting behavioural responses similar to those triggered by perceived predation risk. Whether the same may be true for *Dascyllus* spp. requires further research, though there is evidence that *D. aruanus* show reduced risk-taking at smaller shoal sizes, indicating plasticity in risk-taking behaviour in this genus (Hansen et al., 2016). More diurnal and nocturnal predatory reef fish species have been observed at night on reefs exposed to ALAN (Weschke et al., 2024), meaning that ALAN- and predation-induced activation of the primary stress response may co-occur for genera such as *Dascyllus*. Reducing diurnal activity level, as observed in the present study, may reduce the probability of a predator encounter, though possibly at the cost of diurnal foraging opportunities. In terrestrial vertebrates, ALAN often

alters behaviour in ways that may indirectly influence risk-taking by affecting predator encounters, although direct measurements are rare. Bats commonly aggregate around artificial lights to exploit insect concentrations (Rydell, 2006), and male songbirds exposed to artificial lighting initiate dawn song earlier (Kempenaers et al., 2010). While these behaviours enhance foraging efficiency and have reproductive advantages, respectively, they may also increase predation risk, suggesting a trade-off rather than a straightforward increase or decrease in risk-taking. Overall, the literature suggests that ALAN can affect risk-taking behaviour; however, few studies explicitly quantify risk-taking using standard behavioural assays and after an ecologically relevant exposure duration. Our results highlight a critical knowledge gap in the field, particularly for wild, ecologically relevant exposure in aquatic species.

While evidence exists for mechanisms whereby ALAN exposure may influence risk-taking behaviour in fish directly, the earlier emergence observed in ALAN-exposed fish in the present study may also result from selective mortality on slower-emerging fish. Slower-emerging fish could experience higher mortality due to foraging disadvantages or increased size-dependent predation. Reduced foraging success may limit growth, making them more vulnerable to predators (Lima & Dill, 1990). This effect may be magnified in ALAN-exposed fish due to higher metabolic demands, stress levels, and predator encounters, as discussed above (Georgiou et al., 2024; Kurvers et al., 2018; Weschke et al., 2024). A recent study on a related species *D. flavicaudus* found that young fish exposed to ALAN experienced higher mortality compared to control fish, likely due to increased predation (Schligler, Norin, et al., 2026). Although we found no difference in mass or total length between ALAN and control groups in the present study, larger fish in both treatments were more active and faster to emerge following a chase stimulus, consistent with selection against risk-taking in smaller individuals. We did not collect any form of longitudinal data on individual growth and survivorship, however. Future studies could measure survival and behaviour through time to see if individual behaviour itself is altered in response to ALAN or if fish with certain behaviours have lower survival under ALAN. While our study design does not allow us to separate direct effects of ALAN on behaviour from selective mortality, in either scenario the effects of ALAN on risk-taking behaviour are likely to be ecologically important.

Although risk-taking behaviour has been linked to sociability in fishes (Harcourt et al., 2009; Pike et al., 2008), particularly if increased risk-taking behaviour leads fish to stray

further from a shoal (Conrad et al., 2011), this was not supported in our study. If prolonged exposure to ALAN does cause chronic activation of the primary stress response (Kurvers et al., 2018), it is possible that social species may remain in tight groups following exposure to ALAN. In social species, remaining within social groups has been linked to lower cortisol levels (Culbert et al., 2019). As a result, the physiological effects of ALAN may lead individuals to increase group cohesion and lower individual risk-taking behaviour. In addition, while foraging in groups means resources must be shared among individuals, group foraging may result in a greater number of food items detected or acquired (A. Ward & Webster, 2016b). Individuals may therefore benefit from remaining in groups following ALAN exposure. To our knowledge, no study has previously found effects on sociability following ALAN exposure. It therefore appears that despite the theoretical links with physiological and other behavioural effects of ALAN, there is not yet evidence to support any change in sociability in fishes following ALAN exposure.

In emergence tests, stimulus shoals were kept visible to the focal fish to increase ecological relevance, as *D. trimaculatus* would be unlikely to experience a predation event in isolation. This meant, however, that there was a chance that fish would seek protection in proximity to the conspecific shoal and that this would affect time spent in the shelter of the anemone. While we found no difference in sociability between ALAN and control fish, sociability was significantly reduced following the chase stimulus, indicating that fish were not responding to this stressor by seeking shelter with the shoal. The lack of effect of ALAN on sociability was consistent before and after the chase stimulus. The negative relationship between sociability and fish mass, however, disappeared following the chase stimulus. In emergence trials, there was weak evidence that larger fish remained closer to the shoal irrespective of light treatment. The effects of predation events on behavioural responses often vary according to factors such as experience, sex, and body size (Darby & McGhee, 2019; Herczeg et al., 2016; Roy & Bhat, 2018). However, it has been found that gregarious fish will often seek shelter with a shoal in the presence of a predation threat (Krause & Godin, 1994; Mason et al., 2021). Our results suggest that a simulated predation event elicits the opposite effect in *D. trimaculatus*, with fish moving further from a shoal after chasing, a pattern that is more pronounced in smaller fish. Fish were also less active following a chase stimulus, and the negative effect of ALAN exposure on activity level observed in sociability trials was not present. Reduced activity and sociability following a simulated predator encounter may reflect the species' ecological strategy, as predator evasion on coral reefs often involves seeking refuge within the reef structure

(Boström-Einarsson et al., 2018). Suitable hiding places may be easier to access when alone rather than in a group, and the need for such refugia is likely greater for smaller individuals, which are more vulnerable to predation (Mumby et al., 2006).

While our study provides much-needed data on the effects of ALAN on fish social behaviour, there was considerable variation in fish size among individuals. Although mass was included in all models and was found to influence social behaviour, variation in mass may have affected results in ways that our models could not detect, not least due to variation in treatment exposure duration associated with fish age. As all fish were significantly past the larval phase, however, it is reasonable to assume that they had been subject to chronic exposure to either control or ALAN conditions, though the actual exposure period may have varied. Holding time in the lab also varied, and while this was accounted for in models, it is still worth noting that being held in the lab with lower ALAN levels, no predators, and provision of food may have influenced energy balances and therefore behaviour compared to purely wild exposures to ALAN. Future experiments should therefore aim for greater consistency in size of focal fish and in lab holding time to minimize potential confounding effects. In addition, while we attempted to chase fish for a consistent amount of time (1 min), some fish hid in the anemone before 1 min of chasing was complete. The degree of chasing was considerably below that previously found to be required to elicit exhaustion in similar species (Rummer et al., 2016); however, we cannot rule out that fish behaviour may have been affected by any oxygen debt caused by the chase stimulus (Killen, Norin, et al., 2017). While standardised tests facilitate clearer interpretation of correlations between stimuli and behavioural responses, they may lack ecological relevance and not accurately reflect real predator encounters. In natural settings, how fish respond to actual predator encounters likely influences both the level and form of the physiological stress they experience (Rupia et al., 2016) and thus may affect their recovery. It would be beneficial for future studies to investigate whether the metabolic effects of stimuli may affect risk-taking behaviour. In the present study, while all fish responded to the chase stimulus by moving around the tank, the chase failed to elicit hiding behaviour in some individuals ($n = 7$). The stimulus used is realistic in duration and intensity to ambush or sit-and-pursue predators such as barracuda (Grubich et al., 2008; O'Toole et al., 2010; Porter & Motta, 2004) that are often encountered in the lagoon around Mo'orea but may have failed to elicit hiding in some fish due to the absence of chemical or visual predator cues. Although we were not able to acquire emergence data for

all individuals, our results still indicate effects of ALAN exposure on risk-taking and provide a basis for further research.

Anthropogenic pollutants in aquatic and terrestrial systems are of increasing concern, and therefore have been the target of significant research by ecologists in recent years. Nevertheless, the effects of non-chemical pollutants such as ALAN on social behaviour are relatively underrepresented in the literature (Tiddy, Cortese, et al., 2024). Our study provides the first evidence that exposure to ALAN affects risk-taking behaviour in a marine fish species. We found no effect of ALAN on sociability, consistent with previous work; however, we still recommend this as an area for further study. Also lacking in the literature are studies linking physiological and behavioural effects of ALAN on different species, which would be invaluable for explaining and predicting effects. Our study adds valuable data to the ongoing study of the behavioural effects of anthropogenic pollutants, and indicates likely avenues for further research in this key field.

Chapter 7

General Discussion

7.1. Review of key findings

While evidence exists of effects of anthropogenic stressors on social behaviour in fish species, quantifying the extent of existing knowledge is a key factor in identifying unifying trends. In chapters 2 and 3, therefore, I analyse existing data on how fish sociability and group cohesion are influenced by climate-related stressors and anthropogenic pollutants respectively (Table 7.1). Chapter 2 used a meta-analysis of effect sizes from 36 studies to investigate the effects of temperature, hypoxia, and acidification on fish social behaviour. Meta-analysis revealed no overall effects of temperature or acidification, however group cohesion showed a decline with increasingly severe hypoxia. While effects of climate-related stressors on social behaviour in fishes are evidenced in some studies (e.g., (Angiulli et al., 2020; Davis et al., 2019; Fahlman et al., 2021; Holubová et al., 2021; Maulvault et al., 2018; A. Mitchell et al., 2022)), therefore, these effects only form a unidirectional trend in the case of hypoxia. Chapter 2 also emphasises that more study is needed of climate-related stressors, in particular acidification and stressor combinations. Another striking aspect of the surveyed literature is that no studies investigated both sociability and cohesion in the context of climate-related stressors, meaning no attempts were made to link effects on individuals and groups within the same experimental system.

In chapter 3, I analysed effects of organic, inorganic, and mixed chemical pollutants, noise, light, and turbidity on fish social behaviour, again using effect sizes calculated from the literature. Both organic and inorganic pollutants were associated with reduced sociability, with this effect being concentration-dependent in the case of inorganic pollutants. Interestingly, mixtures of chemical pollutants led to reduced cohesion but increased sociability, possibly as a result of the specific combinations studied. While neither noise nor light exposure had main effects on cohesion, evidence of habituation to prolonged noise exposure was found. Reduced sociability was found in fish exposed to increased light levels, though the majority of these focused on photoperiod or changes in visual conditions, with only one study specifically studying artificial light at night (ALAN). No effect of turbidity on social behaviour was found. These findings indicate a somewhat linear response to chemical pollutants that is perhaps surprising given the number of substances involved. Further study is required, however, particularly into the effects of chemical mixtures and ALAN.

As my findings in chapter 2 indicated, studies of the effects of intra- and interindividual variation in behavioural traits on group dynamics in the context of climate-related stressors are absent from the existing literature on fish social behaviour. In chapters 4 and 5, therefore, I used a model species, rummy nose tetra *Hemigrammus rhodostomus*, to investigate the effects of temperature and hypoxia respectively on links between individual behavioural traits and group dynamics. In chapter 4, individual behavioural traits of activity, sociability, and risk-taking behaviour under three acute temperature treatments were linked to group dynamics of the same fish in groups of 5-6 under the same treatments. In individual trials, fish displayed greater activity, sociability, and risk-taking behaviour under high temperatures. Groups swam faster, were more polarised, and contained a more even distribution of individuals along the group range of motion at higher temperatures. In social, less-active individuals, however, speed and polarisation were reduced at high temperatures, and this was reflected in overall group speed. Groups containing larger fish were more polarised under ambient conditions but became less polarised as temperatures increased. Regardless of temperature, active, less-social fish were found at the front of shoals, with evidence for this being stronger where these individuals also displayed high risk-taking behaviour. These findings show interactions between intra- and interindividual variation and environmental conditions in determining group dynamics and indicate possible mechanisms for non-unidirectional effects of thermal stress on fish social behaviour.

Chapter 5 investigated similar response variables to those in chapter 4, but in the context of hypoxia rather than temperature. Individual and group behaviours were assayed under three oxygen levels, representing normoxia, mild hypoxia, and severe hypoxia. In individual behavioural trials, I found reduced activity under hypoxia but no effect on sociability or risk-taking behaviour. In group trials, severe hypoxia led to reduced speed and polarisation at both the individual and group levels. Interestingly, this was associated with a reduction in interindividual distance, likely mediated by fish reducing their activity and aggregating around shelters placed in the centre of the arena. Fish that displayed greater risk-taking behaviour in individual trials swam faster under hypoxia but moved to the back of shoals when these formed, possibly indicating more time spent swimming alone. The observed reductions in group polarisation under severe hypoxia ($\leq 30\% \text{ O}_2$) reflect the findings of chapter 2, though the effects on interindividual distance (group cohesion) do not. While the findings of chapter 5 indicate that the effects of hypoxia on

social behaviour are largely mediated by changes in activity, I nevertheless find evidence for roles of intra- and interindividual variation in determining behaviour in a group across an oxygen gradient.

In chapter 6, I aimed to address a key knowledge gap identified in chapter 3, namely, the lack of studies of the effects of ALAN on diurnal social behaviour in fish. Taking advantage of an existing study system, I assessed the social and risk-taking behaviour of threespot dascyllus *Dascyllus trimaculatus* exposed since settlement to chronic ALAN in the wild. ALAN-exposed fish were less active in sociability trials but did not differ in sociability from fish exposed to ambient light levels. Following a chase stimulus, however, ALAN-exposed fish took less time to emerge from an anemone, indicating a greater proclivity for risk-taking behaviour in ALAN-exposed fish. Interestingly, these results mirror those of the only known previous study of ALAN on diurnal social behaviour in fish (Kurvers et al., 2018). While two concurring studies is far from conclusive, the results of this chapter echo those of chapter 3 in that further study of the effects of ALAN on fish social behaviour is a key avenue for future work.

Table 7.1. Summary of key fields and knowledge gaps identified prior to the completion of this thesis, key results of this thesis, implications for the field of fish social behaviour, and recommended avenues for future study.

Chapter	Understanding prior to this thesis	Knowledge Gaps	Findings	Implications for gregarious fish	Recommended future directives
2	Social behaviour may be affected by temperature, hypoxia, and acidification via physiological stress responses and alterations to sensory processes.	Empirical evidence of unifying themes in behavioural responses to stressors across species and systems is lacking.	Unidirectional behavioural effects were identified for hypoxia, but not for temperature or acidification. Group cohesion was reduced as oxygen saturation decreased.	Shoaling and schooling species may struggle to maintain cohesion under low oxygen, with potential effects on predation risk, foraging, and social dynamics.	Further studies of the effects of acidification are needed, as are more studies of the effects of hypoxia on sociability. Studies linking individual behavioural responses to changes in group dynamics are highly recommended to explain effects on shoaling and schooling.
3	Anthropogenic pollutants have a range of physiological and stress-related effects on fish social behaviour.	Overarching effects of different pollutant categories and combinations have yet to be examined.	Sociability was reduced in response to individual chemical pollutants and bright light but increased with chemical mixtures. Group cohesion decreased with exposure to chemical mixtures and showed evidence of habituation to noise pollution. Responses to chemical pollutants were largely dose dependent.	Effects on social behaviour differ among pollutant classes and in response to mixtures vs. individual contaminants. Pollutant concentration should be a key consideration for management decisions.	Studies of the effects of a more diverse range of chemical mixtures are required. Non-chemical pollutants, in particular artificial light at night, require further study of acute and chronic effects. Studies of intra- and interindividual variation in response across developmental stages and pollutant levels are recommended.
4	Temperature increases metabolic needs, with evidence for effects on activity and social behaviour	How individual behavioural traits and response to thermal stress may affect dynamics of individuals in groups is unknown.	Temperature affected social behaviour both when alone and in groups. Individual traits dictated roles within groups, and this was in some cases dependent on temperature.	Effects of environmental factors at the group level depend on the individual trait expression of fish within a group.	Repeated measures of behavioural traits across thermal gradients would capture variation in intra-individual response and how this relates to repeatability of roles within groups.
5	Severe hypoxia reduces schooling through changes in activity level and possible interference with sensory processing.	Effects of hypoxia on individual sociability, and how this may be linked to changes in shoaling behaviour, are poorly understood	Activity was reduced in individual behavioural trials under hypoxia. Hypoxia had no effect on sociability. Hypoxia affected speed, polarisation, and cohesion in groups, but these effects were dependent on individual traits.	Activity and leader-follower dynamics appear to affect shoaling under hypoxia, but species ecology likely has a strong effect.	Studies comparing among species and hypoxia treatments may help to quantify variation in coping strategies with regards to activity, and how this translates to social behaviour and shoaling dynamics.
6	Artificial light at night increases metabolic needs through greater nighttime activity and may lead to overactivation of the primary stress response, with implications for growth and fitness.	Effects of ALAN, particularly chronic exposure, on diurnal behavioural traits are largely unknown.	Chronic, wild exposure to ALAN did not affect sociability, but did increase risk-taking behaviour in the form of time to leave a shelter.	Altered response to threats or predation events may increase vulnerability. Increased time spent outside shelters may also exacerbate metabolic effects, though foraging time could be increased.	Integrative studies of physiology and social behaviour are needed to elucidate the mechanisms of changes in behaviour in response to ALAN.

7.2. Contextualising meta-analysis and experimental findings

7.2.1. Temperature

In fish behaviour, as in many areas of science, effects of rising temperatures are of urgent research interest in a world rapidly becoming warmer (Cannon, 2025; Luo et al., 2024; Mukherjee & Bhat, 2024; Schumm et al., 2024). My systematic survey of the literature found that temperature is better studied than both hypoxia and acidification in terms of the number of studies on fish social behaviour. Despite this, meta-analysis revealed no clear trends in behavioural response to high temperatures. The theoretical basis of social behaviour change in ectotherms under high temperatures predicts increased activity associated with higher metabolic rate (Agarwal et al., 2024; Kuruvilla et al., 2023), which may lead to increased risk-taking and lower sociability (Angiulli et al., 2020; Pilakouta et al., 2023). This was supported by my experimental findings in chapter 4 insofar as temperature was associated with increased activity and risk-taking. In contrast to the prediction of higher activity and risk-taking being linked to reduced sociability, sociability was also increased in individual behavioural trials in *H. rhodostomus*. The predicted effect of increased metabolic rate on activity therefore appears to be present in *H. rhodostomus*, however the ways in which this translates to social behaviour are more complex, in line with meta-analysis findings.

While the effects of temperature and other stressors on links between individual traits and group behaviour in fish have not been studied extensively, the complexity of relationships found in chapter 4 are reflected in previous studies of thermal effects on shoaling. In brown trout *Salmo trutta* fry, fish displayed fewer instances of physical contact with a conspecific at low temperatures (6-8°C) compared with at higher (10-12°C) temperatures but tended to remain together following physical contact (Colchen et al., 2016). At 12°C, fish were more likely to immediately move apart following physical contact than at any other temperature. This did not lead to increased nearest neighbour distance (NND), interindividual distance (IID), or variance in interindividual distance at 12°C, suggesting that high temperatures had a greater effect on interindividual interactions within the group than on some metrics of overall group structure. Interestingly, a study on little sand smelt *Atherina boyeri* (*Atherina mochon*) also found increased approach-withdrawal frequency in juvenile fish exposed to high temperatures as eggs and/or larvae (Williams & Coutant, 2003). IID and NND were not measured in this study, but increased approach-withdrawal was in this case associated with lower polarisation and school duration. While the metrics used to assess

shoaling being different makes direct comparison different, it is notable that the effects of interindividual interactions at the shoal or group level appear to vary. In a recent study on crucian carp *Carassius auratus*, increased swimming speeds and synchronisation of swimming speeds at the individual level in group behavioural trials under high temperatures were reflected by increased activity of the group as a whole (Luo et al., 2024). Schooling, however, measured as polarisation, IID, NND, and distance to the group centroid, were not affected. Effects of temperature on social behaviour appear, therefore, to be mediated by factors other than changes in activity in response to elevated metabolic needs.

Even the prediction that an increase in SMR leads to increased activity is not universally evidenced. Careau et al. (2008) proposed a framework of two possible activity responses to increasing SMR: the “performance” model, which predicts increased activity as SMR increases due to high energy throughput and to allow individuals to meet their metabolic needs. The “allocation” model, conversely, predicts that individuals with high metabolic needs may allocate less energy to activity, allowing energy to be conserved for basal metabolic processes (Careau et al., 2008). While Careau et al. (2008) proposed this framework with reference to interindividual differences under a given set of conditions, it may also apply to increased SMR caused by high temperatures (Killen, 2014). A recent study of sheepshead minnow (*Cyprinodon variegatus*) found activity to be negatively correlated with SMR at 22°C, consistent with the “allocation” model, however this correlation disappeared at 32°C (Schumm et al., 2026). While the activity response shown by *H. rhodostomus* in chapter 4 more closely follows the “performance” model, sociability and cohesion were both maintained or increased at high temperatures. The relationships between SMR, activity, and social behaviour under high temperatures appear to vary among species and with degree of stressor exposure, and future studies bridging the gap between physiology and behaviour are needed to elucidate this. Additional stressors often associated with temperature change such as hypoxia and acidification also exert their own physiological effects (Domenici et al., 2017; Jutfelt et al., 2013; Maulvault et al., 2018; A. Mitchell et al., 2022), though very few studies of how this may translate to changes in social behaviour are available.

7.2.2. Hypoxia

As local mechanisms such as eutrophication interact increasingly with global shifts in temperature, periods of low or no oxygen are growing in frequency and severity in aquatic

systems (Baladia et al., 2025; Gattuso et al., 2015). Hypoxia restricts aerobic scope, and in some cases baseline oxygen requirements, in aquatic animals, and thus places physiological constraints on activity and behaviour (Domenici et al., 2017). The themes present in my findings in chapters 2 and 5 broadly support this, as hypoxia reduced swimming speed and polarisation, with greater effects present at oxygen levels at or below 30% saturation. The observed effects of hypoxia on behaviour broadly reflect the ideas of Domenici et al. (2017), in that fish may be able to tolerate low oxygen and maintain cohesive shoaling until a critical point, generally occurring at or below 30% O₂. This appears to generate a more consistent threshold effect on behaviour than that observed in studies of temperature, which is reflected in the greater number of interaction effects with individual traits seen in chapter 4 compared with chapter 5. That being said, behavioural response to hypoxia in group trials in *H. rhodostomus* did vary according to individual traits in chapter 5. In addition, while a reduction in activity was observed in *H. rhodostomus*, this does not represent a universal strategy for coping with hypoxia (Domenici et al., 2013, 2017; Fitzgibbon et al., 2010).

As noted in the introduction to this thesis and discussed in detail by Domenici et al. (2013, 2017) and Chapman and McKenzie (2009), hypoxia is frequently shown to affect activity levels in fish, and activity-based responses have been theorised as falling into two broad categories. Increased activity under hypoxia is thought to be associated with attempts to escape the unfavourable conditions (Domenici et al., 2000; Herbert & Steffensen, 2005; Sommer-Trembo et al., 2017), though it has also been argued that this may represent a non-adaptive “panic” response (Domenici et al., 2013), while reduced activity is consistent with an oxygen-conservation strategy (Alfonso et al., 2020; Cook et al., 2014; Hayes et al., 2019). Which strategy is employed may depend on physiological hypoxia tolerance (Chapman & McKenzie, 2009) and whether hypoxia is escapable (Cook et al., 2014; Herbert et al., 2011). The strategy may also depend on species ecology, with pelagic schooling species being more likely to exhibit increased activity, which can mitigate the exacerbating effects of large shoals on hypoxia while increasing the probability of finding normoxic conditions (Cook et al., 2014; Domenici et al., 2013; Fitzgibbon et al., 2010). The Amazonian streams and wetlands where *H. rhodostomus* are found often experience hypoxic episodes (Luis Val & Wood, 2022) both at night when photosynthetic oxygen production ceases and in stagnant water following floods (Pelster & Wood, 2024). In such situations, where normoxic water may be hard to find, displaying minimal activity but low interindividual distances may allow *H. rhodostomus* to cope with hypoxia while

concurrently benefiting from reduced stress levels (Nadler et al., 2016; Pintos et al., 2024) and predator avoidance by remaining in a group (Cook et al., 2014; Pitcher, 1986).

Alternatively, *H. rhodostomus* may prefer to increase interindividual distances under hypoxia, but prioritised shelter proximity in the behavioural arena used in chapter 5 when not actively shoaling. As a small, littoral species, shelter prioritisation may be selected for in *H. rhodostomus* as a counter-predation measure (Jones et al., 2019).

If reduced interindividual distance in group trials under hypoxia was indeed mediated by fish seeking proximity to shelters. i.e., risk avoidance, this may also explain why I observed increased activity in group trials under hypoxia in fish that displayed greater risk-taking in individual trials. Individuals that display greater risk-taking behaviour may be more vulnerable to predation (Hulthén et al., 2017) but also increase foraging (MacGregor et al., 2021; Planas-Sitjà & Ioannou, 2025), lead groups, and contribute strongly to decision-making (Bevan et al., 2018; Harcourt et al., 2009; Nakayama et al., 2012, 2016; Riley et al., 2025). Interestingly, I also found marginally non-significant evidence that less risk-averse individuals swam near the back of shoals under hypoxia. In chapter 4, less risk-averse individuals tended to be positioned at the front of shoals regardless of the temperature, indicating that risk-taking behaviour may predispose *H. rhodostomus* to group leadership as found in other species (Bevan et al., 2018; Harcourt et al., 2009; Nakayama et al., 2012, 2016). Based on my findings in chapter 5, less risk-averse individuals appear to retain increased risk-taking under hypoxia in a group setting, but this may not translate to group leadership. Leader-follower dynamics, however, rely on decisions made by both leaders and followers (Ioannou et al., 2017; Webster, 2017). Reduced activity and increased tendency to aggregate around shelters under hypoxia may have corresponded to other individuals in shoals being less likely to follow less risk-averse individuals if and when these initiated movements (A. J. W. Ward et al., 2013). If this is the case, a question arises as to whether reducing activity to cope with hypoxia prevents individuals from joining movements, or if reduced proclivity to follow conspecifics when they initiate movement leads to lower activity.

The mechanism of behavioural change under hypoxia is generally ascribed to limitations imposed on aerobic scope and baseline oxygen requirements. There is also evidence, however, that hypoxia can interfere with sensory processing in fish, including olfactory (Tigert et al., 2025) and visual (Country & Jonz, 2021) sensing, and possible impairment of central nervous system functioning (Lu et al., 2005; Lucon-Xiccato et al., 2014; Tigert &

Porteus, 2023). This may mean individuals struggle to rapidly respond to movements made by conspecifics, reducing the efficacy of leader-follower dynamics under hypoxia. As discussed in chapter 2, group size may also have an effect on group speed, polarisation, and cohesion under low oxygen, with the greatest reductions in these being observed in groups of 8-18 individuals. If responses to the movements of shoal mates are delayed or reduced, movements may not propagate through smaller groups, while in larger shoals, the coordination required to shoal cohesively with many other individuals is lacking (Domenici et al., 2017). The mechanisms of movement constraint and initiation/propagation under hypoxia remain, however, unresolved.

7.2.3. Light

Artificial light at night (ALAN) is an emerging anthropogenic pollutant, affecting increasing proportions of ecosystems (Davies et al., 2014; Marangoni et al., 2022). Despite this, studies of how physiological and fitness-related impacts of ALAN may carry over into diurnal behaviour are lacking in fish species. Meta-analysis carried out in chapter 3 revealed a significant effect of light exposure on sociability in fish species, however only one study identified in the literature review explicitly investigated the effects of ALAN (Kurvers et al., 2018). This study found increased risk-taking behaviour, but no effect on sociability, in guppies *Poecilia reticulata*. The remainder of reviewed studies on light focused on behavioural changes associated with changes in brightness (Lafoux et al., 2023; Patch et al., 2022), wavelength (Kelley et al., 2012; Marchesan et al., 2005), or photoperiod (Lucon-Xiccato et al., 2022). While these are ecologically relevant factors, their mechanisms of action likely differ from those of ALAN. Diurnal behavioural effects of ALAN have been proposed to result from increased metabolic needs (Georgiou et al., 2024; Hillyer et al., 2021) and overactivation of the primary stress response (Kurvers et al., 2018), while shoaling behaviour under varying light levels relies on visual stimuli and thus may be improved in brighter light (e.g., Butail et al., 2015; Lafoux et al., 2023; Patch et al., 2022), though lateral line sensing may also play a role (Chaput et al., 2023). Assuming different mechanisms and thus likely different fitness effects, the relative lack of studies of diurnal social behaviour in ALAN-exposed fish is a significant gap in the literature.

While studies of ALAN influencing individual sociability in fish are scarce, no studies of ALAN on fish shoaling or schooling behaviour were found in the review of the literature described in chapter 3. Since this review was published, however, three studies have investigated the effects of ALAN on shoaling. Two of these studies reported reduced inter-

individual distances (increased cohesion) during diurnal shoaling trials following acute ALAN exposure in zebrafish *Danio rerio* (W. Li et al., 2024) and acclimated exposure in mosquitofish *Gambusia holbrooki* (Barzegar et al., 2024) respectively. These findings may indicate that diurnal behavioural responses ALAN exposure in shoaling species are characterised more by social buffering of stress responses (Nadler et al., 2016; Pintos et al., 2024) than by leaving a shoal due to increased risk-taking. The third study reported a marginally non-significant reduction in shoaling in Indian medaka *Oryzias melastigma*, though it is not clear from the study if this refers to diurnal or nocturnal shoaling (Ranjan, 2026). None of these studies investigated effects on individual sociability in addition to shoaling behaviour, though Li et al. (2024) found increased thigmotaxis (anxiety-like behaviour) in ALAN-exposed *D. rerio* both alone and in groups. Increased anxiety-like behaviour is in contrast with the findings of chapter 6 and Kurvers et al. (2018), though this may be a result of acute *versus* acclimated exposure. Whether changes (or lack thereof) in individual sociability in response to ALAN will inform group dynamics within species or study systems therefore remains to be established.

The links between physiological and behavioural effects of ALAN in fish species also lack full understanding, though a number of mechanisms have been proposed. ALAN has been found to affect circadian rhythms in fish, as light level is an essential zeitgeber for fish as for many species (Sánchez-Vázquez et al., 2019). Such disruption has been linked to increased night-time activity (Georgiou et al., 2024) as well as changes in diurnal activity patterns (Pulgar et al., 2019). Stress induction from ALAN exposure may also affect physiology, fitness, and behaviour. In blue-green chromis *Chromis viridis*, ALAN exposure led to increased brain activity, indicated by build-up of metabolites associated with glycolysis and the pentose phosphate pathway, and substances produced by cellular damage and degradation (Hillyer et al., 2021). Hillyer et al. (2021) also found lower levels of gamma-aminobutyric acid (GABA) precursors in the livers of ALAN-exposed *C. viridis*. GABA is an important neurotransmitter with roles in regulating feeding (Snigirov & Sylantsev, 2017), and its receptors are involved in olfactory predator detection and response (Draper & Weissburg, 2019; Nilsson et al., 2012). While there is no empirical evidence that ALAN-exposed fish have altered capacity for olfactory predator detection, *Dascyllus flavicaudus* exposed to ALAN display higher mortality, possibly attributable to increased predation (Schligler, Norin, et al., 2026). There are a number of possible explanations for ALAN-exposed fish suffering higher predator mortality, however, including increased predator encounters mediated by greater night-time activity of both

nocturnal and diurnal predators in sites exposed to ALAN (Weschke et al., 2024). Growing evidence shows that chronically ALAN-exposed fish may be less risk-averse (Kurvers et al., 2018), though whether this is triggered by increased foraging needs, reduced response to predator cues, or selective mortality, as discussed in chapter 6, remains unclear.

7.3. Intra- and interindividual variation in the context of different stressors

Behavioural variation within a social group is a vital component of group dynamics and response to external cues, but to date variation in social behaviour across contexts has been largely studied at the interindividual level in fish. While heterogeneity among individuals has a strong influence on interactions, the degree of ecologically relevant interindividual variation found in a group is inextricably tied to intraindividual phenotypic variation within and across contexts (Biro & Adriaenssens, 2013; Jolles et al., 2019; Jolles, King, et al., 2020; Laskowski & Bell, 2014; D. J. Mitchell & Biro, 2017). My findings in chapters 4 and 5 show evidence of intraindividual variation across abiotic contexts, as individual *H. rhodostomus* became more active, social, and less risk-averse under higher temperatures but less active under hypoxia. Relatively few studies of social behaviour have exposed the same individuals to multiple conditions of temperature (but see (Olla & Studholme, 1971; Pilakouta et al., 2023; Pineda et al., 2020)), though studies of related behaviours have found both intra- and interindividual variation under varying levels of temperature and oxygen (Killen et al., 2012, 2018). In the case of hypoxia, several studies of the effects of progressive hypoxia on shoaling behaviour exist (Cook et al., 2014; Domenici et al., 2002; Hayes et al., 2019; Israeli & Kimmel, 1996; Moss & McFarland, 1970), though these did not explicitly investigate intraindividual variation. It is not entirely clear why exposing the same individuals or groups to variation in conditions appears to be favoured for hypoxia but not for temperature, however this may relate to the period of exposure. Acute exposure was more common for studies of hypoxia (chapter 2), which may allow researchers to sequentially expose individuals to different oxygen concentrations more efficiently. Where the goal is to study variation in traits across contexts, independent treatment groups may miss variation occurring at the intraindividual level (Andreassen et al., 2026; Killen et al., 2012; Norin, 2022; Norin & Gamperl, 2018). Further investigating intraindividual variation in the context of temperature may therefore be an important future research topic.

Just as I observed intraindividual variation across contexts of both temperature and oxygen saturation in *H. rhodostomus*, I also observed changes in how interindividual variation in trait expression related to shoaling behaviour. In some cases, individual traits were not

correlated or were weakly correlated to shoaling behaviour under ambient conditions of temperature and oxygen but gained a stronger influence over group roles and dynamics when conditions changed (Killen et al., 2013). Evidence for an effect of individual sociability and activity on speed and polarisation of fish in groups was magnified at higher temperatures, and risk-taking behaviour was associated with swimming speed and position in the shoal under hypoxia but not normoxia. Interindividual differences in behaviour may be muted in groups under ambient conditions (Guayasamin et al., 2017; Herbert-Read et al., 2013; MacGregor et al., 2021) particularly in species such as *H. rhodostomus* with a strong tendency to school (Lafoux et al., 2024; Lei et al., 2020). In stressful conditions, however, interindividual differences may be amplified leading to greater expressions of heterogeneity within the group (Jolles, King, et al., 2020; Killen, Adriaenssens, et al., 2016; Killen et al., 2011). This could reflect individuals experiencing different levels of physiological stress or adopting different strategies for coping with physiological stress (Domenici et al., 2013, 2017; Killen, Cortese, et al., 2021) and may result in group fragmentation or reduce cohesion and polarisation (Jolles, King, et al., 2020; Killen, Marras, et al., 2017). While a reduction in cohesion did not appear to affect *H. rhodostomus* exposed to thermal or hypoxia stress, the extent to which individual traits informed roles in groups still changed. Stressful environments may magnify heterogeneity within a group, but social species will also deviate from individual physiological and energetic optima to remain with conspecifics (Cooper et al., 2018; Tiddy et al., 2025). Desire to remain with conspecifics under stressful conditions may make individuals more likely to mirror the behaviour of conspecifics exhibiting strong behavioural trends, leading to greater influence of, for example, more social or less risk-averse individuals (Jolles, King, et al., 2020).

Although the extent to which variation among individual *H. rhodostomus* informed group dynamics varied across contexts, it is not completely clear how much of this is due to intraindividual variation in trait expression among social contexts. Put another way, it is not clear how much of this modulation was due to individuals changing their behaviour when alone but continuing to occupy the same roles and positions in groups, or vice versa. The social environment is a strong modifier of behaviour (Killen et al., 2026; Tiddy et al., 2025; Ward et al., 2007; Webster & Ward, 2011) and may also play a role in how individuals respond physiologically to stressors (Killen et al., 2026). While individuals changed their behaviour in response to stressors both when alone and in groups, I did not measure repeatability within or across contexts due to time constraints and it is thus not

clear whether individuals remained consistent in the behavioural trait expression relative to the trait expression of shoalmates. As individuals fulfilling certain roles in groups may come under varying selection pressures (Ioannou & Dall, 2016; Jolles, King, et al., 2020) and may affect the behaviour and subsequent fitness of other individuals in the group (Bevan et al., 2018; Hulthén et al., 2017), this is an interesting question in a world increasingly characterised by unprecedented changes in abiotic conditions (Bevacqua et al., 2025; Cannon, 2025; Orr et al., 2024). If intraindividual behavioural variation as a trait is repeatable, and its influence on the role of individuals in a group is similarly consistent, intraindividual behavioural variation may reveal itself as a major target for selection and a vital avenue for future research (Andreassen et al., 2026; Schumm et al., 2026).

7.4. Limitations and avenues for further study

The work done in this thesis aimed to identify and begin to fill gaps in understanding of the effects of anthropogenic stressors on fish social behaviour. Inevitably, many opportunities for future research were identified that did not fall within the scope of this thesis. Chapters 2 and 3 emphasise the low number of existing studies on stressors such as acidification, ALAN, and turbidity, the bias toward studies of shoaling over individual traits in the context of hypoxia and noise, and the overall lack of literature surrounding effects of stressor combinations. It should be noted, however, that some studies of multiple stressors have been recently published and therefore were not included in chapters 2 and 3 (Allibhai et al., 2023; Cominassi et al., 2025; Zanghi et al., 2023). Studies also represent a relatively small fraction of known fish species, meaning phylogenetic signal among studies is hard to detect and interpret. While I focus here on the limitations of the experimental data presented in chapters 4-6 and the future avenues for research suggested by these, a number of other study areas within fish social behaviour are data deficient, and these are discussed in more detail in chapters 2 and 3.

While chapters 4 and 5 present a novel perspective on the effects of temperature and hypoxia on fish behaviour, logistical limitations prevented the experiments described in these chapters from being combined as a full-factorial study. To date, only one study exists that has investigated the effects of temperature and hypoxia in combination on social behaviour in fish (Pineda et al., 2020). This study found no effect of the combination of temperature and hypoxia on social group cohesion; however, this was measured in an air-breathing species, the bronze corydoras *Corydoras aeneus* (Pineda et al., 2020). It is reasonable to expect that non-air-breathing species may respond differently to the

combination of stressors, due to differences in vulnerability and coping strategy under hypoxic conditions (Chapman & McKenzie, 2009; Domenici et al., 2013). The findings of chapters 4 and 5 underscore the relevance of combining stressors, as the trends found in response to temperature and hypoxia were markedly different in *H. rhodostomus*. It is possible therefore that temperature in combination with hypoxia would have an antagonistic effect on behaviour in non-airbreathing species, but it is not clear how this would translate to links between behavioural expression across social contexts. A direct next step following on from the work presented in chapters 4 and 5 would therefore be to conduct a full-factorial experiment linking intra- and interindividual behavioural variation with group dynamics across levels of both temperature and hypoxia.

Across chapters 4-6, I focused on variation within and among individuals in response to abiotic stressors. Time and logistical constraints prevented me, however, from acquiring repeated measures for individuals or groups across (chapters 4 and 5) or within contexts (chapter 6). While repeated measures are an essential part of establishing personalities, there are issues associated with repeating the same test on the same individual. Fish may become habituated to stimuli (Lucon-Xiccato et al., 2023), or repeated exposure to changes in temperature or oxygen levels may allow some level of plastic acclimation (Killen, Adriaenssens, et al., 2016; Thalmann et al., 2025). Nevertheless, many of the trends identified in this thesis would form a more robust basis for future studies of the role of intra- and interindividual variation if repeatability could be established. If the links identified here between individual and group behaviours and how these are influenced by the abiotic environment are found to be repeatable, this may help to elucidate variation in response to stressors across species and groups (Careau et al., 2008; Killen et al., 2012; Schumm et al., 2026). Repeatable correlations with physiological stress responses may also reveal patterns in how physiological effects translate to effects on social behaviour, which in the case of some stressors is still unclear.

Although the physiological bases of activity changes under temperature and hypoxia are relatively well-studied (Cook et al., 2014; Domenici et al., 2017; Ioannou, 2017; Killen, Cortese, et al., 2021; Lucon-Xiccato et al., 2014), how these relate to changes in shoaling and related behaviours is less clear. I was unable to obtain physiological data for *H. rhodostomus* as part of the experiments carried out in chapters 4 and 5 due to time constraints, however linking physiological responses with intra- and interindividual behavioural variation and shoaling dynamics would be an extremely valuable next step.

Schumm et al. (2026) found that asocial behaviour, i.e., time spent not associating with a shoal, was positively correlated with SMR in *C. variegatus* acclimated near the middle of the species thermal range (22°C) but was negatively correlated with SMR under summertime temperatures (32°C). This study used separate treatment groups for each temperature acclimation; therefore, it is not known whether the same pattern would occur if individuals were tested under both conditions, i.e., intraindividual variation in the relationship between SMR and sociability. In European sea bass *Dicentrarchus labrax*, however, a relationship between activity and risk-taking behaviours and routine metabolic rate (RMR) was found in severe hypoxia, but not when the same individuals were tested under normoxia or mild hypoxia (Killen et al., 2012). The physiological basis for social behaviour and possibly shoaling may therefore vary across contexts, even within the same individuals (Killen et al., 2012). Further studies of this effect across species may have ramifications for our ability to predict behavioural changes across environmental contexts (Killen, Cortese, et al., 2021). This would be particularly valuable for stressors such as temperature with non-linear effects on behaviour, and for understudied stressors such as ALAN.

Although the physiological and fitness effects of ALAN on fish species are becoming increasingly well-evidenced (Hillyer et al., 2021; Pulgar et al., 2019; Schligler et al., 2021; Schligler, Norin, et al., 2026; Schligler, Roost, et al., 2026), how these effects translate to changes in behaviour remains somewhat understudied (Bassi et al., 2022). Further studies of physiology alongside social behaviour are therefore strongly warranted, including both overall metabolic rate measures (Pulgar et al., 2019) and detailed studies of metabolomics (Hillyer et al., 2021). The GABA signalling pathway in particular may have implications for foraging (Snigirov & Sylantyev, 2017) and predator avoidance (Draper & Weissburg, 2019), both of which are linked to social behaviour (Pitcher, 1986; Pitcher et al., 1982), and has been found to be affected by ALAN in a reef fish, as discussed above (Hillyer et al., 2021). Another interesting effect identified by Hillyer et al. (2021) is evidence of increased brain activity in ALAN-exposed fish. While this may simply be a product of increased wakefulness, studies of the effects of ALAN on cognition in fish have found impaired learning (Lucon-Xiccato et al., 2023), cognitive flexibility (De Russi et al., 2024), and decision-making (Pulgar et al., 2023). Linking physiological changes in brain activity with cognitive processing and behavioural changes is a potentially significant area for future research, therefore.

7.5. Conclusions

The effects of anthropogenic stressors on natural systems are more apparent than ever before. As organisms seek to cope with a broad range of stressors, behavioural flexibility is a vital mechanism by which animals may respond to changes in their environment. This thesis sought to consolidate the existing literature on the effects of anthropogenic stressors on fish social behaviour, to identify major knowledge gaps, and to begin to address some of these gaps. Meta-analysis of the current literature revealed effects of hypoxia, chemical pollutants, light level, and noise on social behaviour in fishes. Studies of multiple stressors in combination were lacking, as were studies of artificial light at night (ALAN), an emerging stressor. In addition, no studies included in literature reviews had incorporated effects of anthropogenic stressors into investigating links between individual behavioural traits and group dynamics. Two subsequent chapters of this thesis therefore aimed to investigate how intra- and interindividual trait variation across environmental contexts shape the roles of individuals with known traits in groups, and group dynamics. Effects of individual traits were apparent in the shoaling dynamics of *Hemigrammus rhodostomus*, as were effects of increasing temperature and moderate-to-severe hypoxia. Fundamentally, the effects of individual traits were also modulated by both temperature and hypoxia, revealing novel evidence for the role of intra- and interindividual variation in determining shoaling dynamics across environmental contexts in gregarious species. The final data chapter of this thesis sought to address another gap in the literature: the lack of studies of ALAN. In a coral reef fish *Dascyllus trimaculatus*, wild, chronic ALAN exposure was associated with increased diurnal risk-taking behaviour but no effect on sociability. While the mechanisms of diurnal behavioural change in ALAN-exposed fish are still not entirely clear, this adds to the growing body of evidence for behavioural effects of ALAN on fish species. While my findings on the effects of climate-related stressors on social dynamics in *H. rhodostomus* and of ALAN on risk-taking behaviour in *D. trimaculatus* begin to address key research gaps identified earlier in this thesis, there remain a number of exciting avenues for future work on the effects of anthropogenic stressors on fish social behaviour. In particular, my findings highlight the relevance of exploring variation in phenotypes both within and among individuals and further demonstrate the importance of the social environment when considering the effects of anthropogenic stressors. Exploring the complex dynamics of fish social behaviour is a challenge and a privilege, and this thesis joins the growing body of work seeking to understand how our activities as humans continue to affect this fascinating system.

Appendices

Supplementary Materials: Chapter 3

Supplementary Table 3.1. Results of papers investigating effects of pollutants on sociability and group cohesion. Reduced/increased sociability/group cohesion indicates reduction/increase in all measured metrics of group cohesion under at least one treatment. “Results” shows the reported results from each study per stressor and metric tested. “Results summary” shows the overall result from each study based on effect size calculated as part of meta-analysis, as shown in Figure 3.4. Where effect size could not be calculated for a study, the reported result is given, indicated by “reported”. – indicates a negative effect on social behaviour, + indicates a positive effect, and 0 indicates no significant effect. * after study citation indicates some or all data required for calculating treatment effect sizes could not be obtained for this study.

Pollutant type	Metric	Paper	Species	Substance	Treatments	Results	Results summary
Organic	Sociability + cohesion	Al Marshoudi et al. 2023	<i>Danio rerio</i>	Aged microplastics, virgin microplastics	0, 1000 ppm	No effect on group cohesion. Reduced sociability with aged but not virgin microplastics	–
		Hong et al. 2021	<i>Danio rerio</i>	Fluoxetine hydrochloride, citalopram hydrobromide, venlafaxine hydrochloride, amitriptyline hydrochloride, sertraline hydrochloride, vortioxetine, paroxetine hydrochloride, fluvoxamine maleate Acetylsalicylic acid, ibuprofen, naproxen, bezafibrate, clofibrate, gemfibrozil	0, 0.1, 1, 10, 100, 1000 µg l ⁻¹	Reduced sociability and increased cohesion following exposure to most antidepressants, no effect of paroxetine hydrochloride on sociability, reduced cohesion with amitriptyline and sertraline. No effect of most medicines on TCS, increased TCS with acetylsalicylic acid. Increased IID with acetylsalicylic acid and naproxen, reduced with others. No effect of ibuprofen	+
		Khursigara et al. 2021	<i>Sciaenops ocellatus</i>	Oil	200 ppm	No effect on maximum group size, TCS, or DtCS	+
		Lei et al. 2022	<i>Danio rerio</i>	Deltamethrin	0, 0.03, 0.1, 0.333 µg l ⁻¹	Increased TCS, increased NND and IID at 0.03 µg l ⁻¹ , reduced NND and IID at 0.01 µg l ⁻¹ , increased NND at 0.333 µg l ⁻¹	0
		Lin et al. 2022	<i>Danio rerio</i>	Ammonia	0, 90000, 180000 µg l ⁻¹	Increased IID, no effect on TCS or time in far zone	–
		Salahinejad et al. 2022a	<i>Danio rerio</i>	Bisphenol-S	0, 1, 10, 30 µg l ⁻¹	Increased IID and DCS, no effect on number of excursions from group.	–

Organic				Ethinylestradiol (EE ₂)	1 µg l ⁻¹	Increased IID and DCS, no effect on number of excursions from group.	
		Salahinejad et al. 2022b	<i>Danio rerio</i>	Bisphenol-S	Maternal exposure (0, 1, 10, 30 µg l ⁻¹)	Reduced IID (10 µg l ⁻¹) and TCS (1 µg l ⁻¹), increased number of excursions (30 µg l ⁻¹), no effect on ACS.	–
		Sarasamma et al. 2020	<i>Danio rerio</i>	EE ₂	Maternal exposure (1 µg l ⁻¹)	Increased number of excursions from shoal	
	Sociability	Abreu et al. 2016	<i>Rhamdia quelen</i>	Fluoxetine hydrochloride	0, 50 µg l ⁻¹	No effect on sociability	+
		Adedara et al. 2022	<i>Danio rerio</i>	Perfluorooctanoic acid	0, 250, 500, 1000 µg l ⁻¹	No effect on sociability	+
		Altenhofen et al. 2019	<i>Danio rerio</i>	2,2-dichlorovinyl-dimethylphosphate	0, 1000, 5000, 10000 µg l ⁻¹	No effect on sociability	–
		Ansai et al. 2016	<i>Oryzias latipes</i>	Fluoxetine hydrochloride	0, 100 µg l ⁻¹	Increased latency to first contact, reduced number of contacts. No effect on time in contact or distance to conspecifics	–
		Barcellos et al. 2020	<i>Danio rerio</i>	Aripiprazole	0, 0.000556, 0.00556, 0.556 µg l ⁻¹	Fewer approaches to shoal at 0.556 µg l ⁻¹ ; no effect on time spent or distance travelled near shoal	0
		Bertram et al. 2018	<i>Gambusia holbrooki</i>	17b-trenbolone	0, 0.016 µg l ⁻¹	Reduced TCS and sociability score, increased approaches to shoal, no effect on latency to approach shoal	0
		Brodin et al. 2013	<i>Perca fluviatilis</i>	Oxazepam	0, 1, 1000 µg l ⁻¹	Reduced sociability	–
		Brodin et al. 2017	<i>Rutilus rutilus</i>	Oxazepam	0, 0.84, 200 µg l ⁻¹	No effect on sociability	0
		Burman 2019 (thesis)	<i>Gasterosteus aculeatus</i>	Oxazepam	0, 40 µg l ⁻¹	No effect on sociability	–
		Calcagno et al. 2016	<i>Jenynsia multidentata</i>	Carbamazepine	0, 10, 50, 200 µg l ⁻¹	No effect on sociability	–
		Calvo 2016 (Thesis)	<i>Poecilia reticulata</i>	Oxazepam	0, 100 µg l ⁻¹	No effect on sociability	–
		Cervený et al. 2020	<i>Perca fluviatilis</i>	Oxazepam, bromazepam, temazepam, clobazam, combination	0, 0.5, 8 µg l ⁻¹	No effect on sociability	–
		Chen et al. 2023	<i>Danio rerio</i>	Penicillin	0, 10 µg l ⁻¹ 0, 5 ppm	Fewer approaches to shoal More approaches to shoal with O ₃ -polystyrene	0

Organic	Sociability			Polystyrene, UV-treated polystyrene, O ₃ -treated polystyrene			
		Correia et al. 2019	<i>Danio rerio</i>	Carbaryl	0, 10, 100, 1000 µg l ⁻¹	No effect on sociability	+
		Correia et al. 2022	<i>Danio rerio</i>	Fluoxetine hydrochloride	0, 0.1, 1, 10 µg l ⁻¹	No effect on sociability	+
		Dong et al. 2018	<i>Carassius auratus</i>	Hexabromo-cyclododecane	0, 2, 20, 200 µg l ⁻¹	Less time away from shoal at 200 µg l ⁻¹ , no effect on times leaving shoal	+
		Fenske et al. 2020	<i>Danio rerio</i>	17α-ethinylestradiol	0, 0.0005 0.0015, 0.005 0.05, 0.075 µg l ⁻¹	Reduced TCS and ACS after chronic (15d) exposure, no effect of acute (1h) exposure or on time in far zone	–
		Giacomini et al. 2016	<i>Danio rerio</i>	Fluoxetine hydrochloride	0, 16, 50 µg l ⁻¹	Reduced TCS, no effect on ACS, time in far zone, or number of entries to far zone	–
		Jacquín et al. 2017	<i>Poecilia reticulata</i>	Oil	0, 500000 ppm, wild exposure clean/polluted	No effect on TCS	0
		Kaplan et al. 2013*	<i>Fundulus heteroclitus</i>	BBP	0, 100 µg l ⁻¹	Less time with large shoal, more time with small shoal and away from both shoals	– reported
		Kellner et al. 2016	<i>Gasterosteus aculeatus</i>	Citalopram	0, 0.09, 1.5 µg l ⁻¹	No effect on latency to leave, times leaving, or time away from shoal	0
		Ligocki et al. 2019	<i>Gambusia affinis</i>	Bifenthrin	0, 0.001, 0.003, 0.006, 0.012, 0.025 µg l ⁻¹	No effect on ACS or TCS	+
		Liu et al. 2018	<i>Danio rerio</i>	Triclosan, 2,4,6-trichlorophenol (2,4,6-TCP), 2,4-dichlorophenol (2,4-DCP); mixture ratio 1:2:4	0, 140, 280, 560 µg l ⁻¹	Reduced ACS, TCS and DCS	–
		Liu et al., 2017	<i>Carassius carassius</i>	Erythromycin, Ketoconazole	0, 2 µg l ⁻¹ 0, 0.2, 2, 20 µg l ⁻¹ All combinations	Less time away from shoal and less transitions away from shoal with ketoconazole alone, no effect of erythromycin or combination	+
		Lucon-Xiccato et al. 2023	<i>Danio rerio</i>	Triclocarban	0, 5, 50 µg l ⁻¹	No effect on sociability score at 5 µg l ⁻¹ , increased sociability score at 50 µg l ⁻¹	+
		Mancia et al. 2023	<i>Danio rerio</i>	Virgin microplastics, environmentally contaminated microplastics	0, 400 µg l ⁻¹	No effect on social preference	0
		Martin et al. 2019	<i>Gambusia holbrooki</i>	Fluoxetine hydrochloride	0, 0.06, 0.35 µg l ⁻¹	No effect on sociability score or TCS	+
		Mason et al. 2021	<i>Poecilia reticulata</i>	Fluoxetine hydrochloride	0, 0.04, 0.36 µg l ⁻¹ (maternal exposure)	Increased TCS in paired trials at 0.36 µg l ⁻¹ , no effect on time with large shoal	0
		Maulvault et al. 2018	<i>Argyrosomus regius</i>	Venlafaxine hydrochloride	0, 160 µg l ⁻¹ (fed), 20 µg l ⁻¹ (solution)	Reduced TCS. Reduced LCS (fed). No effect on ACS.	–

Organic	Sociability						
		McCallum et al. 2017*	<i>Neogobius melanostomus</i>	Fluoxetine hydrochloride	0, 1, 40 µg l ⁻¹	No effect on TCS	No effect reported
		Meijide et al. 2018	<i>Gambusia holbrooki</i>	Fluoxetine hydrochloride	0, 1, 5, 25, 50 µg l ⁻¹	No effect on TCS	+
		Moriera & Luchiari 2022	<i>Danio rerio</i>	Oxybenzone	0, 10, 100, 1000 µg l ⁻¹	Lower TCS at 10 µg l ⁻¹ . No effect on LCS	–
		Orjes et al. 2015 (thesis)	<i>Carassius carassius</i>	Fluoxetine hydrochloride	0.1, 1, 100 µg l ⁻¹	No effect on TCS	+
		Petersen et al., 2021	<i>Danio rerio</i>	Ciprofloxacin, ceftazidime, chlortetracycline	0, 6250 µg l ⁻¹	No effect on time near shoal, time away from shoal, or mean distance from shoal	0
		Porseryd et al. 2017a	<i>Danio rerio</i>	Citalopram	0, 0.0001 µg l ⁻¹	Fewer times leaving shoal, no effect on latency to leave or time away	+
				17α-ethinylestradiol	0, 0.002, 0.007 µg l ⁻¹	Fewer times leaving shoal, no effect on latency to leave or time away	
		Porseryd et al. 2017b	<i>Danio rerio</i>	EE ₂	0.4, 0.0009 µg l ⁻¹	No effect on sociability	+
		Porseryd et al. 2019	<i>Gasterosteus aculeatus</i>	EE ₂	0.004, 0.03 µg l ⁻¹	Increased latency to leave shoal, fewer times leaving shoal	+
		Qiu et al. 2020	<i>Gobiocypris rarus</i>	P-chloroaniline	0, 10, 19, 29, 38 mg l ⁻¹	Reduced TCS	–
				3-aminobenzoic acid ethyl estermethanesulfonate (MS222)	0, 11, 23, 34, 45 mg l ⁻¹	Reduced TCS	
				Cadmium	0, 3, 7, 10, 13 mg l ⁻¹	Reduced TCS	
		Renick 2014* (thesis)	<i>Fundulus heteroclitus</i>	Chlorpyrifos	0, 1, 5 µg l ⁻¹	Increased DCS	– reported
		Reyhani et al. 2011	<i>Danio rerio</i>	EE ₂	0, 0.005, 0.025 µg l ⁻¹	Increased latency to leave a shoal, fewer times leaving shoal, less time away from shoal	0
		Sancho Santos et al. 2021	<i>Squalius cephalus</i>	Tramadol hydrochloride	0, 1 µg l ⁻¹	Increased distance to conspecific	–
		Santos et al. 2023	<i>Danio rerio</i>	Caffeine	0, 0.5, 1.5, 300 µg l ⁻¹	Reduced time swimming near conspecific shoal, increased approaches to conspecific shoal. No effect on time spent with or away from shoal, or number of entries to far zone	–
		Sun et al. 2020	<i>Danio rerio</i>	Diclofenac	0, 1.09, 104 µg l ⁻¹	Increased TCS	+
					30 mg l ⁻¹		

Organic	Sociability			Aquatic colloids		Increased TCS	
		Sunedin 2015 (Thesis)	<i>Gasterosteus aculeatus</i>	Oxazepam, fexofenadine, mixture	0, 2 µg l ⁻¹	No effect on sociability score	0
		Takai et al. 2022	<i>Oryzias latipes</i>	Diazepam	0, 26, 255 µg l ⁻¹	Increased number of times leaving shoal with both	–
				Microplastics	9900000 ppm		
		Tamagno et al. 2022	<i>Danio rerio</i>	EE2	0, 0.00005, 0.0005, 0.005, 0.05, 0.075 µg l ⁻¹	Increased time near shoal and reduced time away from shoal with acclimated (15d) exposure, increased time near shoal but no effect on time away from shoal with acute (1h) exposure	+
		Volkova et al. 2015	<i>Danio rerio</i>	EE ₂	0, 0.0012, 0.0016 µg l ⁻¹ 0, 0.0012 µg l ⁻¹ (parental exposure)	Increased latency to leave social zone, fewer entries and less time in far zone (direct exposure). No effect of parental exposure	0
		Xia et al. 2010	<i>Danio rerio</i>	Nonylphenol	0, 0.1, 1, 10, 50, 100 µg l ⁻¹	No effect on times leaving shoal, reduced TCS at 100 µg l ⁻¹	–
		Zang et al. 2019	<i>Danio rerio</i>	Triclosan	0, 20000 µg l ⁻¹	No effect on distance travelled near a conspecific shoal	+
		Zhang et al. 2017	<i>Danio rerio</i>	2,2',4,4'-tetrabromodiphenyl ether (BDE-47)	0, 1.63, 241 µg l ⁻¹	Increased number of contacts and contact time with no recovery time. No effect on number of contacts, reduced average contact time in one trial (4d) with 2-6d recovery	+
	Group cohesion	Aimon et al. 2022	<i>Dicentrarchus labrax</i>	Oil	0, 400ppm	No effect on group cohesion	+
		Alfonso et al. 2020	<i>Dicentrarchus labrax</i>	Ammonia	0, 3, 7, 11, 15 µg l ⁻¹	Reduced group cohesion at ≥ 11 µg l ⁻¹	0
		Armstrong et al. 2019	<i>Micropogonias undulatus</i>	Oil	0, 0.006, 0.032 ppm	Reduced group cohesion at 0.032 ppm	–
		Barry 2012	<i>Aphanius dispar</i>	Fluoxetine hydrochloride	0, 0.03, 0.3, 3 µg l ⁻¹	Increased swimming speed relative to nearest neighbour at 0.03 µg l ⁻¹ , no effect on NND	0
		Chen et al. 2021a	<i>Danio rerio</i>	Tetrabromobisphenol A (TBBPA)	0, 1.09 µg l ⁻¹	Reduced cohesion, no effect on sociability	–
		Chen et al. 2022	<i>Cyprinus carpio</i>	Glyphosate Polyethylene microplastics	0, 5000, 15000 µg l ⁻¹ glyphosate, 0, 1500, 4500 µg l ⁻¹ microplastics,	No effect on number of interactions between fish	0
		Eslava-Mocha et al. 2019*	<i>Piaractus brachypomus</i>	Polyethyloxylated tallow amine POEA-TA15	0, 200, 500, 1000, 2000, 4000, 8000, 16000, 32000, 70000, 140000 µg l ⁻¹	Less cohesive schooling pattern	– reported

Organic	Group cohesion	Fahlman et al. 2021	<i>Perca fluviatilis</i>	Oxazepam	0, 14.9 µg l ⁻¹	Reduced NND	+
		Faria et al. 2021	<i>Danio rerio</i>	Glyphosate (N-phosphonomethyl-glycine)	0, 0.27, 3.38 µg l ⁻¹	Reduced IID and maximum interfish distance	+
		Hamilton et al. 2018	<i>Anchoa lamprotaenia</i> , <i>A. lyolepis</i>	SKF 38393 hydrochloride, SCH 23390 hydrochloride	0, 1000, 10000 µg l ⁻¹	No effect on NND or IID	+
		Hamilton et al. 2022	<i>Danio rerio</i>	Benzo[a]pyrene	0, 252.3, 2523, 25230 µg l ⁻¹	Increased IID at 25230 µg l ⁻¹	0
		Holcombe et al. 1980*	<i>Pimephales promelas</i>	2,4-dichlorophenol, 2,4-dichlorophenol + NaOH	8230, 8450, 7430 + NaOH, 12330 + NaOH µg l ⁻¹	No effect on schooling pattern	No effect reported
		Huang et al. 2021	<i>Danio rerio</i>	Deltamethrin	0, 15 µg l ⁻¹	Increased IID after 2h exposure	+
		Johansen et al., 2017	<i>Pomacentrus amboinensis</i> , <i>Pomacentrus moluccensis</i>	Oil	0, 0.0025, 0.0057 ppm	Reduced shoal size in both species at 0.0057 ppm	–
		Khalil et al. 2013	<i>Oryzias latipes</i>	Chlorpyrifos	0, 12 µg l ⁻¹	Reduced solitary duration at 8d exposure. No effect at 4d exposure. No effect on solitary frequency, shoaling or schooling frequency or duration	+
		Khalil et al. 2017	<i>Oryzias latipes</i>	Chlorpyrifos	0, 12, 120 µg l ⁻¹	Reduced shoaling & schooling frequency & duration, increased solitary duration. No effect on solitary frequency	–
		Lal et al. 1984*	<i>Cirrhinus mrigala</i>	Alkyl benzene sulphonate	0, 0.015 µg l ⁻¹	No effect on schooling pattern	No effect reported
		Lanzarin et al. 2020	<i>Danio rerio</i>	Glyphosate (N-phosphonomethyl-glycine)	0, 1320, 1940, 5030 µg l ⁻¹	No effect on NND or IID	–
		Leite et al. 2023	<i>Luciobarbus bocagei</i> <i>Alburnus alburnus</i>	Esfenvalerate	0, 1.2, 2 µg l ⁻¹	Reduced cohesion index in <i>L. bocagei</i> , no effect on <i>A. alburnus</i>	–
		Mattson et al. 2018	<i>Carassius carassius</i>	Polystyrene	Food chain exposure	Reduced IID	+
		Nakayama et al. 2005	<i>Oryzias latipes</i>	Polychlorinated biphenols (PCBs)	0, 1, 5, 25, 125 µg l ⁻¹	Increased NND at 25 µg l ⁻¹ . No effect on MDCS, time in shoal, or polarity	–
		Qiu et al. 2022	<i>Danio rerio</i>	Amitriptyline	0, 2.5, 40 µg l ⁻¹	Reduced frequency and duration of schooling following 21d recovery, increased duration of schooling with no recovery.	0
		Saglio & Trijasse 1998	<i>Carassius auratus</i>	Atrazine, diuron	0, 0.5, 5, 50 µg l ⁻¹ (static water)	Fewer fish shoaling in static treatments. No effect on flow treatments	–

Organic	Group cohesion				0, 0.1, 1, 10 µg l ⁻¹ (flowing water)		
		Saglio et al. 2001	<i>Carassius auratus</i>	Prochloraz, bentazone, nicosulfuron	0, 10, 100, 1000, 10000 µg l ⁻¹	No effect on grouping behaviour	0
		Saglio et al. 2003	<i>Carassius auratus</i>	Prochloraz	0, 25, 50, 100 µg l ⁻¹	Increased grouping behaviour at 4-6d exposure; no effect at 2 and 8d	+
		Santos et al. 2020	<i>Danio rerio</i>	Microplastics	2 ppm	No effect on IID or NND	+
		Santos et al. 2021	<i>Danio rerio</i>	Microplastics	2 ppm	No effect on IID or NND	+
		Schmidel et al. 2014	<i>Danio rerio</i>	Atrazine	0, 10, 1000 µg l ⁻¹	No effect of 10 µg l ⁻¹ , increased IID, NND, furthest neighbour distance, and shoal area, and reduced contacts and cohesion index at 1000 µg l ⁻¹	–
		Ward et al. 2008*	<i>Fundulus diaphanus</i>	4-nonylphenol	0, 1 µg l ⁻¹	Increased NND	–
		Weis & Weis 1974a	<i>Menidia menidia</i>	Sevin	0, 0.1 µg l ⁻¹	Increased school area, no effect on polarity	–
		Weis & Weis 1974b*	<i>Carassius auratus</i>	Dichloro-diphenyl-trichloroethane (DDT)	0, 1 µg l ⁻¹	Increase school area at 3d exposure, reduced polarity and 3-7d exposure. No effect at 1 and 14d	– reported
		Williams 1989*	<i>Dicentrarchus labrax</i>	Methyl parathion	0, 2500, 5000, 10000 µg l ⁻¹	Increased duration of approach-orientation at 5000 µg l ⁻¹ 24h exposure; reduced duration of parallel orientation, reduced frequency of realignment	– reported
		Yofukuji et al. 2021	<i>Moenkhausia forestii</i>	Sugarcane ash	0, 800 mg l ⁻¹	No effect on number of isolated individuals	–
		Zhang et al. 2018	<i>Danio rerio</i>	6-OH-BDE-47 6-MeO-BDE-47	0, 1.31, 7.03 µg l ⁻¹ 0, 1.64, 12.6 µg l ⁻¹	No effect on time per contact Reduced time per contact at 6d exposure (no effect at 5d)	–
Inorganic	Sociability + cohesion	Al Marshoudi et al. 2023	<i>Danio rerio</i>	Cadmium	0, 50 µg l ⁻¹	No effect on sociability or group cohesion	–
		Zhang et al. 2016	<i>Gobiocypris rarus</i>	Tributyltin	0, 0.88, 9.2, 93 ng l ⁻¹	Reduced cluster score, latency to leave shoal, and movements away from shoal. Increased time away from shoal	–
		Attaran et al. 2019	<i>Danio rerio</i>	Selenomethionine	0, 2.1, 11.6, 31.5 µg l ⁻¹	Reduced sociability at ≥11.6 µg l ⁻¹ , no effect on group cohesion	0
		Attaran et al. 2021	<i>Danio rerio</i>	Selenomethionine	3.6, 12.8, 34.1 µg l ⁻¹	Reduced sociability at 34.1 µg l ⁻¹	–
		Bowser 2021 (Thesis)	<i>Fundulus heteroclitus</i>	Arsenic	0, 10, 500 ppb	No effect on sociability	–

Inorganic	Sociability	Capriello et al. 2021	<i>Danio rerio</i>	Aluminium	0, 11000 µg l ⁻¹	Reduced sociability at 15d exposure, no effect at 10d and 20d	–
		Chen et al. 2021b	<i>Danio rerio</i>	Titanium dioxide (TiO ₂) nanoparticles	0, 100, 1000 µg l ⁻¹	Increased time in social (mirror) zone	0
		da Silva Acosta et al. 2016	<i>Danio rerio</i>	Copper	0, 5, 9, 20, 60 µg l ⁻¹	No effect on time spent near conspecific shoal	+
		Qiu et al. 2020	<i>Gobiocypris rarus</i>	Cadmium	0, 3000, 7000, 10000, 13000 µg l ⁻¹	Reduced TCS	–
		Vogt et al. 2013	<i>Heterandria formosa</i>	Copper	1, 25, 50, 100 µg l ⁻¹ (2h or 7d exposure)	Reduced TCS and increased time to first shoaling in acute exposure (2h), no effect in chronic exposure (7d)	–
		Ward et al. 2013	<i>Morone americana</i>	Copper	0, 5 µg l ⁻¹	No effect on sociability	–
	Group cohesion	Chen et al. 2021a	<i>Danio rerio</i>	Titanium dioxide (TiO ₂)	0, 100 µg l ⁻¹	Reduced time in contact but no effect on rate of contacts	–
		David et al. 2015*	<i>Labeo rohita</i>	Sodium cyanide	0, 280, 285, 290, 295, 300, 305, 310, 315, 320, 325, 330 µg l ⁻¹	Less cohesive schooling pattern	– reported
		Huang et al. 2021	<i>Danio rerio</i>	Cadmium	0, 3500 µg l ⁻¹	Reduced IID at 1-2h exposure	0
		Iwama et al. 1986*	<i>Oncorhynchus tshawytscha</i>	Sodium pentachlorophenate	0, 3.9, 39 µg l ⁻¹	Less cohesive schooling at 39 µg l ⁻¹	– reported
		Koltes, 1985	<i>Menidia menidia</i>	Copper	0, 100 µg l ⁻¹	Reduced NND, no effect on polarity	+
		Lu et al. 2017	<i>Danio rerio</i>	Zinc	0, 10000, 20000, 30000 µg l ⁻¹	Reduced IID, no effect on shoal area with zinc. No effect of chromium	+
				Chromium	12500, 25000, 40000 µg l ⁻¹		
		Ososkov & Weis 1996	<i>Fundulus heteroclitus</i>	Methylmercury	0, 5, 10 µg l ⁻¹ Clean & polluted origin fish (0, 11.2 µg l ⁻¹ wild exposure)	Reduced IID and increased polarity (polluted origin); increased polarity (clean origin). Increased IID & polarity in polluted vs. clean origin fish	+
		Petitjean et al. 2021*	<i>Gobio occitaniae</i>	Cadmium + copper + zinc	0.007/0.62/4.06, 13.5/9.96/551 µg l ⁻¹	No effect on NND or number of contacts	No effect reported
		Santos et al. 2023	<i>Danio rerio</i>	Zinc	0, 10000, 20000, 30000 µg l ⁻¹	Reduced IID with zinc, no effect of chromium or on shoal area	+
				Chromium	0, 12500, 25000, 40000 µg l ⁻¹		

Inorganic	Group cohesion	Santos et al. 2020	<i>Danio rerio</i>	Copper	2, 17.1, 51.9, 131 $\mu\text{g l}^{-1}$	No effect on IID or NND	+
		Santos et al. 2021	<i>Danio rerio</i>	Copper	2.42, 52.9, 133 $\mu\text{g l}^{-1}$	No effect on IID or NND	+
		Shelton et al., 2023	<i>Danio rerio</i>	Cadmium	Two of six fish exposed to 0, 1 $\mu\text{g l}^{-1}$	No effect on NND or shoal size	0
		Zhao et al. 2020	<i>Danio rerio</i>	Lead	0, 4.5, 9.62, 18.6 $\mu\text{g l}^{-1}$	Increased number of contacts at 18.6 $\mu\text{g l}^{-1}$	+
Mixture	Sociability + cohesion	Al Marshoudi et al. 2023	<i>Danio rerio</i>	Cadmium + microplastics	0, 50 $\mu\text{g l}^{-1}$ + 1000 ppm	No effect on sociability or group cohesion	–
	Sociability	Alfonso et al. 2022	<i>Danio rerio</i>	PCBs & PBDEs	0, 1.93 $\mu\text{g l}^{-1}$	No effect on sociability	–
		Bailey & Levin 2015	<i>Danio rerio</i>	Firemaster 550	10, 100, 1000, 3000 $\mu\text{g l}^{-1}$	Reduced sociability following 5d exposure with 40d recovery and 1d exposure with no recovery. No effect of 1d exposure with 7d recovery	–
		Cervený et al. 2020	<i>Perca fluviatilis</i>	Oxazepam + bromazepam + temazepam + clobazam	0, 0.5 each, 8 each $\mu\text{g l}^{-1}$	No effect on sociability	–
		Chagas et al. 2019	<i>Danio rerio</i>	Tannery effluent	0, 1000000, 3000000 $\mu\text{g l}^{-1}$	Increased ACS, increased TCS at 3000000 $\mu\text{g l}^{-1}$	+
		Chen et al. 2023	<i>Danio rerio</i>	O ₃ -treated polystyrene + penicillin	0, 5 ppm + 10 $\mu\text{g l}^{-1}$	More approaches to shoal with O ₃ -polystyrene and O ₃ -polystyrene with penicillin.	0
		Mehdi et al. 2022*	<i>Pimephales promelas</i>	Wastewater	250000000, 500000000 $\mu\text{g l}^{-1}$	Less time interacting with conspecific at 5e8 $\mu\text{g l}^{-1}$. No effect on TCS.	–
		Porseryd et al. 2017b	<i>Danio rerio</i>	EE ₂ + citalopram	0.0009 + 0.0001 $\mu\text{g l}^{-1}$ citalopram	No effect on sociability	+
		Sun et al. 2020	<i>Danio rerio</i>	Diclofenac + aquatic colloids	0, 0.9, 96.3 $\mu\text{g l}^{-1}$ + 30 mg l^{-1}	Increased TCS	+
		Takai et al. 2022	<i>Oryzias latipes</i>	Diazepam + microplastics	0.026 $\mu\text{g l}^{-1}$ + 9900000 ppm	Increased number of times leaving shoal	–
		Toft et al. 2015	<i>Gambusia holbrooki</i>	Paper mill effluent	Wild exposure	Reduced attending and positioning behaviour	–
		Ward et al. 2013	<i>Morone americana</i>	Copper + 4-nonylphenol	0, 2 + 5 $\mu\text{g l}^{-1}$	No effect on sociability	+
	Group cohesion	Chen et al. 2021a	<i>Danio rerio</i>	Tetrabromobisphenol A (TBBPA) + Titanium dioxide (TiO ₂),	0, 1.09 $\mu\text{g l}^{-1}$ + 100 $\mu\text{g l}^{-1}$	Reduced time in contact but no effect on rate of contacts	–
		Chen et al. 2022	<i>Cyprinus carpio</i>	Glyphosate + microplastics	0, 5000, 15000 $\mu\text{g l}^{-1}$ glyphosate + 0, 1500, 4500 $\mu\text{g l}^{-1}$ microplastics,	No effect on number of interactions between fish	0

Light		Santos et al. 2020	<i>Danio rerio</i>	Copper + microplastics	15, 60, 125 µg l ⁻¹ + 2ppm	Reduced NND and IID at 125 µg l ⁻¹	+
		Santos et al. 2021	<i>Danio rerio</i>	Copper + microplastics	2.42, 52.9, 133 µg l ⁻¹ + 2ppm	No effect on IID or NND	+
	Sociability	Kurvers et al. 2018	<i>Poecilia reticulata</i>		24h 5000 lx, 12h 5000 lx 12h 0.5 lx, 12h 5000 lx, 12h 0 lx	No effect on TCS	0
		Lucon-Xiccato et al. 2022	<i>Oryzias latipes</i>	8h:16h light/dark; 16h:8h light/dark	0, 900 lx	Reduced TCS in second half of trial	0
		Matchette et al. 2021	<i>Gasterosteus aculeatus</i>	Visual noise	Statics, slow, medium, fast	No effect on larger shoal choice, reduced DCS	+
		Zhang et al. 2017	<i>Danio rerio</i>	Day/night	0, 900 lx	No effect on number of contacts or average contact time	–
	Group cohesion	Bierbach et al. 2018	<i>Poecilia mexicana</i>		6000 lx	Reduced cohesion with live conspecific, no effect with robot conspecific	+
		Burbano Lombano et al. 2022	<i>Danio rerio</i>		0, 250 lx	Reduced IID with and without flow, increased polarity with flow	+
		Butail et al. 2015	<i>Devario aequipinnatus</i>	Bright-to-dark, dark-to-bright	1, 250 lx	Increased group cohesion	+
		Chaput et al. 2022	<i>Danio rerio</i>	Day/night	0, 900 lx	Increased cohesion	+
		Clark 2022 (thesis)	<i>Gasterosteus aculeatus</i>	White noise	2057.5, 5132.6, 6797.3, 8512.4 lx	Reduced cohesion	–
		Fahlman et al. 2021	<i>Perca fluviatilis</i>	Day/night	0, 900 lx	No effect on group cohesion	–
		Kelley et al. 2012	<i>Melanotaenia australis</i>	Neutral filter, yellow filter	0.616, 0.449lx	Higher IID with yellow filter, no effect of neutral filter	–
		Khait et al. 2009	<i>Mormyrus probosciostris</i>		0.18, 237 lx	Increased NND in light at 49 and 65d exposure, reduced NND at 245d	0
		Lafoux et al. 2023*	<i>Hemigrammus rhodostomus</i>	Day/night	0, 900 lx	Increased IID and NND, reduced polarity	– reported
		Marchesan et al. 2005	<i>Dicentrarchus labrax</i> , <i>Mugil cephalus</i> , <i>Lithognathus</i>	Increasing or decreasing light level; increasing or decreasing wavelength	0.2-680 lx 410-650 nm	Increased cohesion in light in <i>L. mormyrus</i> and <i>S. aurata</i> . Increased cohesion at higher wavelengths in <i>M. cephalus</i> . Reduced cohesion in light and under increasing wavelength in <i>Di. labrax</i> ; increasing cohesion under reducing wavelength	0

Light	Group cohesion		<i>mormyrus, Sparus aurata</i>				
		Neo et al. 2018*	<i>Dicentrarchus labrax</i>	Day/night	0, 900 lx	Reduced IID in light	+ reported
		Olla & Studholme 1971	<i>Pomatomus saltatrix</i>	Day/night	0, 900 lx	Increased sociability index	+
		Patch et al. 2022*	<i>Astyanax mexicanus</i>		0, 32 lx	Increased polarity	+ reported
		Ryer & Olla 1998	<i>Gadus chalcogrammus</i>	12h light 12h dark Gradual light reduction	0, 21 lx 0-39 lx	Reduced NND in both treatments	+
		Sogard & Olla 1996	<i>Gadus chalcogrammus</i>		0.3, 40 lx	Reduced NND and cohesion index	+
		Zhang et al. 2018	<i>Danio rerio</i>	Day/night	0, 900 lx	No effect on cohesion	0
		Zhao et al. 2020	<i>Danio rerio</i>	Day/night	0, 900 lx	Fewer but longer contacts in light vs. dark (0 $\mu\text{g l}^{-1}$)	0
Noise	Sociability	Hanache et al. 2018	<i>Phoxinus phoxinus</i>	Boat noise	25, 35 dB	No effect on distance to conspecific	+
	Group cohesion	Clark 2022 (thesis)	<i>Gasterosteus aculeatus</i>	White noise	108.5, 135 dB	No effect on cohesion	+
		Currie 2021 (thesis)*	<i>Rutilus rutilus</i>	Simulated background noise, pulse tone	110, 145 dB	No effect on cohesion	+
			<i>Cyprinus carpio</i>	Artificial ambient sound, white noise	110, 121, 130 dB	Increased cohesion	
		Currie et al. 2020	<i>Phoxinus phoxinus</i>	Sinewave 150Hz	72, 155 dB continuous, slow, intermediate, fast pulses	No effect on cohesion	+
		Currie et al. 2021	<i>Phoxinus phoxinus</i>	Sinewave tones, octave band noise,	80, 150 dB 150, 2200 Hz	No effect on MDCS. Reduced orientation angle (increased cohesion) at 2200Hz sinewave tone noise	+
		Duarte et al. 2019	<i>Leporinus taeniatus</i>	Hydroelectric turbine noise	Ambient, 100dB	More unpolarized fish, no effect on polarized fish	0
		Fewtrell and McCauley 2012*	<i>Pagrus auratus</i>	Air gun	100, 185 dB	No effect on schooling pattern	No effect reported
		Ginnaw et al. 2020	<i>Gasterosteus aculeatus</i>	Acoustic playback	108, 123 dB	No effect on NND, polarity or heading (inverse polarity)	+
		Herbert-Read et al. 2017	<i>Dicentrarchus labrax</i>	Pile-driving sound	116, 129 dB	Reduced polarity (heading), no effect on NND or MDCS	+

Noise	Group cohesion	Hubert et al. 2020	<i>Dicentrarchus labrax</i>	Brown noise	123, 163 dB	No effect on IID	–
		Kastelein et al. 2017*	<i>Dicentrarchus labrax</i>	Pile-driving sound	130, 136, 142, 148, 154, 160, 166 dB	Reduced IID at 148 vs. 136 dB	+ reported
		Kok et al. 2021	<i>Gadus morhua</i>	Seismic survey, pile-driving	95, 195 dB 78, 172 dB	Greater cohesion under both noise treatments	+
		Mauro et al. 2020	<i>Sparus aurata</i>	White noise	115, 145 dB 63, 125, 500, 1000 Hz	Reduced school area	–
		Neo et al. 2014*	<i>Dicentrarchus labrax</i>	Brown noise (continuous/intermittent)	115, 165, 172 dB	No effect on NND	No effect reported
		Neo et al. 2015a	<i>Danio rerio</i>	White noise (continuous, intermittent 1-1, intermittent 1-9, intermittent irregular)	89, 112 dB	Reduced IID with intermittent 1-1 noise	+
		Neo et al. 2015b*	<i>Dicentrarchus labrax</i>	Brown noise (0.25, 0.5, 1, 2 pps)	104, 158 dB	Reduced IID at 1pps	+ reported
		Neo et al. 2016	<i>Dicentrarchus labrax</i>	Brown noise (continuous, impulsive regular, impulsive irregular, impulsive regular with ramp-up)	108, 167 (continuous), 186 (impulsive)	No effect on IID	+
		Neo et al. 2018	<i>Dicentrarchus labrax</i>	Brown noise	100, 192 dB	No effect on group cohesion	+
		Rojas et al. 2023*	<i>Rutilus rutilus</i>	Motorboat noise	92 dB (control), not reported	Increased shoal area	– reported
		Short et al. 2020	<i>Phoxinus phoxinus</i>	Random noise	Not reported (control), 152 dB	Increased standard deviation of fish location	+
		van der Knaap et al. 2022*	<i>Clupea pallasii</i> , <i>Oncorhynchus gorboscha</i> , <i>Oncorhynchus keta</i>	Motorboat noise	105, 117, 123, 146 dB	Increased school cohesion in all species	+ reported
		Voellmy et al. 2014	<i>Phoxinus phoxinus</i>	Cargo ship noise	70, 115 dB	No effect on number of contacts	+
	Sociability	Fischer et al. 2013	<i>Gasterosteus aculeatus</i>	Green algae	0, 0.016 NTU	No effect on TCS, reduced preference for larger shoal and fewer changes between shoals	–
		Kimbell & Morrell 2016	<i>Pungitius pungitius</i>	Algae	0, 12.5 NTU	Less time spent with similarly sized conspecifics, no effect on TCS	0

Turbidity	Group cohesion	Aspbury et al. 2019	<i>Etheostoma fonticola</i>	Light filters	0, 40 NTU	Reduced preference for large conspecifics, no effect on time interacting with a conspecific	–
		Borner 2016 (thesis)	<i>Poecilia reticulata</i>	Clay	0, 300, 800 NTU	Increased IID but reduced time alone in clear source fish. Reduced IID but fewer initiated associations in turbid fish source fish	–
		Borner et al. 2015	<i>Poecilia reticulata</i>	Clay	0, 850 NTU	Reduced group cohesion	–
		Clark 2022 (thesis)	<i>Gasterosteus aculeatus</i>	White noise	2.72, 5.25, 13.09, 36.43 NTU	No effect on cohesion	+
		Ehlman et al. 2019*	<i>Gambusia affinis</i>	Clay	0, 20, 40 NTU	No effect on IID or number of nearest neighbours	No effect reported
		Gray et al. 2014	<i>Notropis anogenus</i> , <i>N. bifrenatus</i> , <i>N. heterodon</i> , <i>N. heterolepsis</i> , <i>N. volucellus</i>		0.33, 0.61, 1.53, 1.58, 2.1, 2.45, 2.99, 3.84, 4.65, 5.70, 6.97 NTU	Reduced proportion of fish shoaling in <i>N. anogenus</i> and <i>N. bifrenatus</i> . No effect on other species	–
		Kimbell & Morrell 2015a	<i>Poecilia reticulata</i>	Clay	0, 50, 100, 200 NTU	Increased IID at 100 and 200 NTU	–
		Kimbell & Morrell 2015b	<i>Poecilia reticulata</i>	Algae	0, 20 NTU	No effect on number of near neighbours	0
		Langenhof et al. 2016	<i>Gasterosteus aculeatus</i>		0.05, 57, 66, 75, 93, 111, 138 NTU	No effect on number of fish within one BL	+
		Macpherson 1998	<i>Diplodus puntazzo</i> , <i>D. sargus</i> , <i>D. vulgaris</i>		10, 20 NTU	No effect on shoal size	–
		Michael et al. 2021	<i>Cyprinella lutrensis</i> , <i>Notropis stramineus</i>	Clay	0, 100, 250 NTU	Increased NND and shoal area	–
		Ohata et al. 2014	<i>Engraulis japonicus</i> , <i>Plecoglossus altivelis</i> , <i>Seriola quinqueradiata</i>	Kaolin clay	0, 1.5, 5.8, 14.6, 87.7 NTU	Increased polarity in <i>E. japonicus</i> and <i>P. altivelis</i> , reduced NND in <i>P. altivelis</i> and <i>S. quinqueradiata</i> at 5.8-14.6 NTU, increased NND at 87.7 NTU in <i>S. quinqueradiata</i>	+
		Suriyampola et al. 2018	<i>Danio rerio</i>	Clay	1, 60.1 NTU	No effect on MDCS	+

TCS = time near conspecific shoal; IID = inter-individual distance; DtCS = distance travelled near a conspecific shoal; NND = nearest neighbour distance; ACS = approaches to a conspecific shoal; DCS = distance to a conspecific shoal; LCS = latency to approach a conspecific shoal; MDCS = mean distance to the centre of the shoal. NTU = nephelometric turbidity units.

Supplementary Table 3.2. Results of phylogeny-adjusted MCMCglmm on the effects of organic contaminants on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	<i>p</i> MCMC
Intercept	-0.349	-4.805	3.870	2400	0.856
Pollutant concentration (zscore)	-0.029	-0.152	0.089	2400	0.633
Group size	-0.011	-0.057	0.036	2400	0.653
Replicates	0.007	-0.003	0.017	2400	0.203
Exposure period (days)	-0.001	-0.002	0.001	2400	0.433
Metric (sociability)	-0.483	-0.784	-0.208	2603	< 0.01**
Exposure type (Acute)	0.023	-0.190	0.267	2400	0.831
Exposure type (Developmental)	-0.347	-0.994	0.319	2400	0.316
Exposure type (Parental)	-0.066	-0.712	0.603	2400	0.836
Zscore*metric	-0.084	-0.344	0.192	2400	0.531

Supplementary Table 3.3. Results of phylogeny-adjusted MCMCglmm on the effects of inorganic contaminants on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	<i>p</i> MCMC
Intercept	-0.002	-3.680	3.900	2400	0.969
Pollutant concentration (zscore)	0.054	-0.144	0.257	2400	0.589
Group size	-0.080	-0.183	0.023	2201	0.116
Replicates	-0.004	-0.013	0.005	2400	0.345
Exposure period (days)	0.001	-0.030	0.042	2214	0.903
Metric (sociability)	-0.434	-0.993	0.175	2065	0.143
Exposure type (Acute)	-0.480	-1.237	0.330	2499	0.239
Exposure type (Developmental)	-1.663	-2.712	-0.493	2400	< 0.01**
Exposure type (Parental)	-1.242	-4.315	1.330	2179	0.433

Exposure type (Uncontrolled)	-0.248	-3.889	2.797	2206	0.989
Zscore*metric	-1.453	-2.117	-0.710	2400	< 0.001***

Supplementary Table 3.4. Results of phylogeny-adjusted MCMCglmm on the effects of mixed contaminants on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	<i>p</i> MCMC
Intercept	-43.71	-75.51	-10.68	396.0	< 0.01**
Pollutant concentration (zscore)	-117.6	-205.2	-34.54	396.0	< 0.01**
Group size	-0.242	-0.400	-0.078	436.6	< 0.01**
Replicates	0.002	-0.035	0.033	396.0	0.914
Exposure period (days)	0.000	-0.007	0.006	273.8	0.970
Metric (sociability)	44.27	11.07	76.65	396.0	< 0.01**
Exposure type (Acute)	-0.668	-1.176	-0.136	396.0	< 0.01**
Exposure type (Developmental)	-0.394	-1.121	0.237	396.0	0.217
Exposure type (Parental)	-0.151	-1.379	1.163	396.0	0.793
Exposure type (Uncontrolled)	-2.557	-3.830	-0.750	396.0	< 0.01**
Zscore*metric	118.6	35.49	206.2	396.0	< 0.01**

Supplementary Table 3.5. Results of phylogeny-adjusted MCMCglmm on the effects of noise on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	<i>p</i> MCMC
Intercept	-0.100	-2.609	2.815	1867	0.663
Noise level (dB)	-0.001	-0.012	0.010	1867	0.931
Group size	-0.064	-0.164	0.037	1867	0.213
Replicates	0.017	-0.017	0.056	1867	0.366
Exposure period (days)	-4.043	-6.969	-1.144	1867	< 0.01**
Metric (sociability)	-1.150	-4.479	2.348	1932	0.481

Exposure type (Uncontrolled)	406.0	118.3	699.5	1867	< 0.01**
Noise level*metric	0.037	-0.025	0.099	1867	0.245

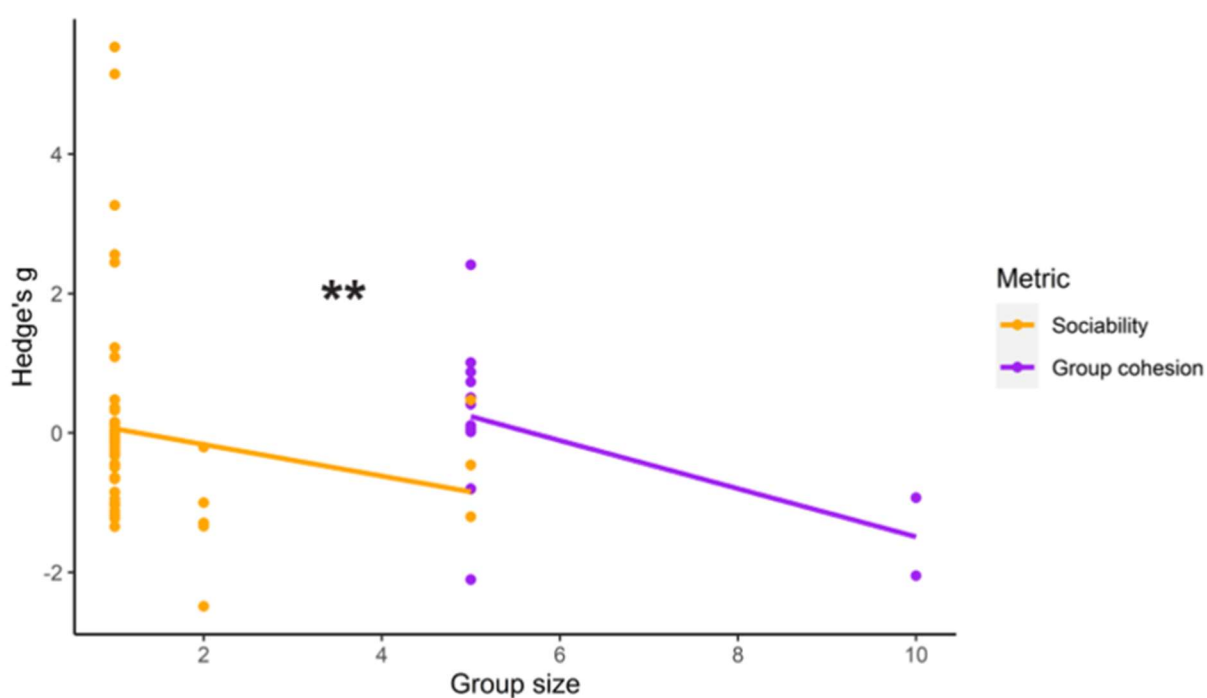
Supplementary Table 3.6. Results of phylogeny-adjusted MCMCglmm on the effects of light on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	<i>p</i> MCMC
Intercept	4.116	-8.003	17.51	1867	0.477
Light level	0.000	-0.001	0.001	1453	0.982
Group size	-0.349	-0.858	0.104	129.5	0.126
Replicates	-0.195	-0.403	0.019	399.5	0.077
Exposure period (days)	0.052	-0.049	0.165	1651	0.300
Metric (sociability)	-3.038	-5.041	-1.227	1160	< 0.01**
Exposure type (Acute)	0.178	-1.441	1.868	1867	0.830
Exposure type (Uncontrolled)	-7.378	-21.28	7.030	819.6	0.309
Treatment (lx or nm)	3.252	-1.146	7.858	1713	0.163
Light exposure*metric	0.00002	-0.001	0.001	1741	0.967
Light exposure*treatment	-0.006	-0.014	0.002	1717	0.168

Supplementary Table 3.7. Results of phylogeny-adjusted MCMCglmm on the effects of turbidity on sociability and group cohesion.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	<i>p</i> MCMC
Intercept	0.409	-13.06	13.24	1595	0.960
Turbidity (NTU)	-0.002	-0.004	0.000	1867	0.097
Group size	0.001	-0.027	0.029	2010	0.961
Replicates	-0.054	-0.139	0.033	1867	0.227
Exposure period (days)	-0.021	-0.189	0.159	1192	0.807
Metric (sociability)	1.337	-14.24	17.26	136.1	0.876

Exposure type (Acute)	0.756	-0.523	1.997	1011	0.247
Exposure type (Parental)	8.832	-55.96	70.88	844.8	0.769
Exposure type (Uncontrolled)	3.127	-18.50	25.70	263.1	0.806
Turbidity*metric	0.001	-0.158	0.154	1867	0.997



Supplementary Figure 3.1. Variation in effects of mixed chemical pollutants on sociability and group cohesion in fish species according to group size. ** indicates $p < 0.01$.

Supplementary Methods

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 “pollution”, “contaminant”, “noise”, “light” or “turbidity” with the terms “social* behaviour”, “sociability” or “group cohesion”, and the term “fish” (Google Scholar only) (Figure 3.1). Searches were limited to English language studies and those within the field of zoology. Papers used included those published in peer-reviewed journal articles as well as unpublished theses (5.5%). Relevant papers that were missed by literature searches were also identified from citations (Alfonso et al., 2020; Fahlman et al., 2021; Salahinejad et al., 2022). Sources were only included for analyses if shoaling or schooling were examined in relation to anthropogenic contaminants and pollutants, including chemical contaminants, noise, light, and turbidity. Analysis was therefore limited to species that are known to exhibit shoaling or schooling behaviour. Where species were not specified as shoaling or

schooling in relevant papers e.g., in trials of individual sociability or aggregation, searches of the literature were conducted to ascertain whether each species displays shoaling or schooling behaviour. As this review focused on effects on fish species, studies of chemical compounds not designed to test the effects of toxicants in aquatic systems, such as use of zebrafish *Danio rerio* as pharmacological models, were excluded (Wiprich et al., 2020). 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-anthropogenic stressors (e.g., predation cues) were also excluded. Interactions with temperature were included, as fish are ectothermic and therefore particularly dependent on environmental temperature for determining rates of a variety of relevant physiological processes; evidence exists of additive effects of temperature with contaminants on fish physiology (Morgan et al., 2001). Papers using numerical models (theoretical studies) were excluded, as were conspecific vs. heterospecific preference tests. Papers studying “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; Clark & Ioannou, 2022). 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.

Data collection

Following paper inclusion, data on the following variables were collected for each paper. In full factorial studies, which was the case for all but two (Holcombe et al., 1980; Porseryd et al., 2017) papers investigating interactions between multiple contaminants and/or pollutants, the effects of individual- and multiple-stressor trials were recorded separately.

- a) Effect size of each treatment on cohesion or sociability, relative to the control. As studies used different metrics to assess sociability and 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 standardize difference of means between groups) of treatments (i.e. contaminant or pollutant exposure) were calculated for 141 studies and 1816 treatments, as some or all treatments from 24 studies (Currie, 2021; David et al., 2015; Ehlman et al., 2019; Eslava-Mocha et al., 2019; Fahlman et al., 2021; Fewtrell & McCauley, 2012; Holcombe et al., 1980; Iwama et al., 1986; Kaplan et al., 2013; Kastelein et al., 2017; Lafoux et al., 2023; Lal et al., 1984; McCallum et al., 2017; Mehdi et al., 2022; Neo et al., 2014; Neo, Ufkes, et al., 2015; Patch et al., 2022; Petitjean et al., 2021; V. M. Renick, 2014; Rojas et al., 2023; van der Knaap et al., 2022; A. J. W. Ward et al., 2008; Weis & Weis, 1974; Williams, 1989) were excluded where some or all data needed to calculate effect size was not available. Effect sizes were calculated as a standardized measure of change in sociability or 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 cohesion or

sociability, so that positive effect sizes indicate an increase in sociability or cohesion and negative effect sizes a decrease. Effect size of each treatment (Cohen's d) on each metric of cohesion or sociability were calculated according to the formula:

$$Cd = \frac{\bar{x}_1 - \bar{x}_2}{PSD}$$

Where Cd is Cohen's d , $\bar{x}$ is the mean of each group, and PSD is the pooled standard deviation of both groups, calculated as:

$$PSD = \sqrt{\frac{(N^1 - 1)SD_1^2 + (N^2 - 1)SD_2^2}{N^1 + N^2 - 2}}$$

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:

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

Where standard error rather than standard deviation was reported in a paper, standard deviation was calculated according to:

$$\sigma = SE\sqrt{n}$$

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

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

Where median and quartile values were reported, these were used in place of mean and standard deviation according to (Greco et al., 2015). Effect size was calculated for each treatment level, e.g. 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 e.g., across time scale, means at each sampling point were recorded and used to calculate the overall mean and SD. Raw data was used to calculate means and standard deviations if these were not reported in the paper. Where exact values were not reported and raw data was not available, data was extracted from graphs

using WebPlotDigitizer version 4.6 (Rohatgi, 2022). For forest plot construction, mean and standard error of effect size for each study was calculated from effect sizes calculated for all treatment levels.

- b) Focal species used in each paper. Species names differed in some studies from the modern accepted scientific name; in these cases, the modern 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.
- c) Class of contaminant or pollutant to which fish were exposed. Among non-chemical pollutants, noise, light, and turbidity were included. Classes of chemical contaminants were organic (including medicines, organically derived pesticides, oil and oil derivatives including microplastics, and androgens), inorganic (metals and metal salts), and mixed. Mixed contaminants included both contaminants of unspecified makeup, such as industrial or agricultural effluent, and specific combinations of contaminants used in lab settings.
- d) Treatment levels of variables of interest. For trials with more than one treatment level, 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 wild population comparisons. For combined stressors, effect size for all trials with non-control values of both or all stressors were calculated relative to trials using control values for both or all stressors. Where treatments were introduced partway through/comparative to different control treatments, changes were compared by subtracting Hedges g values for control before vs. after from treatment before vs. after trials (Morris, 2008). Where this was not possible due to data presentation, values from after treatment introduction were compared to the control. Actual (not nominal) treatment levels were recorded where these were given. For fluctuating treatments, the effect size was calculated between control and the maximum treatment level. As different contaminants may produce effects at different concentrations, variation in concentration was high for many substances. Treatment levels were therefore converted to z scores using the formula:

$$z = \frac{x - \bar{x}}{\sigma}$$

Where x is the value, $\bar{x}$ is the mean, and σ is the standard deviation of the mean.

- e) Group sizes. This was defined as the number of fish used per group trial in group cohesion studies. Where group size varied, the minimum number of fish per group in a treatment was used. It was not possible to use an average number due to the way group numbers were reported in some papers.
- f) Sex of fish(es) used in each experiment. This was recorded as unsexed where fish were not separated by sex, or where reported data was pooled for both sexes.
- g) Number of replicates. Number of replicates was recorded as number of groups per treatment. Where the number of replicates per treatment varied e.g., between control and treatment groups, the 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 per group was used as the calculations used do not allow a sample size of one.

- h) Period over which fishes were exposed to each treatment. Exposure time was recorded in days, with appropriate fractions for hours and minutes (e.g., 1h = $1/24 = 0.0417$ 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.
- i) Exposure type. While related to exposure period, this allowed us to separate wild and lab studies, and direct exposure from developmental or parental exposure. 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. Developmental studies were defined as those where fish were exposed during the egg and/or larval phase, then allowed to grow into adults before behavioural trials were conducted. Parental exposure was defined as parents of tested fish being exposed, but not the tested fish themselves. Acute exposure was defined as up to seven days direct exposure of adult or juvenile fish, while acclimated exposure was defined as seven days or more direct exposure of adult or juvenile fish.
- j) Metrics used to assess cohesion or sociability. In the majority of studies, individual sociability was quantified using some variant of the three-chamber test (Xia et al., 2010) or shoal preference test (Al Marshoudi et al., 2023; Salahinejad et al., 2022), while group cohesion 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, nearest-neighbour distance, shoal polarity, or mean distance from the centre of the shoal (Table 3.1). Individual sociability was often measured as the frequency of approach to a conspecific shoal, time spent near a conspecific shoal, latency to approach a conspecific shoal, or distance from a conspecific shoal (Table 3.1). 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 3.1). 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 experimental arenas were divided into only two zones, and was only used if it was the only variable reported, being directly proportional to time in social zone. “Time in far zone” was used in studies in which arenas were divided into three or more zones, and refers to farthest zone from the stimulus shoal. Where zone times were statistically compared e.g., near vs. 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 e.g., if fish spent more time near the shoal in the control treatment, but had no preference in other treatments.

- k) Reported statistical significance (or lack thereof) of the effect of each treatment were recorded for each paper. Statistical significance was recorded as $p < 0.05$. 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.
- l) Country where each study was carried out (geographical location).

Statistical analysis

A meta-analysis was then carried out in R using the MCMCglmm package (Hadfield, 2010) to run phylogenetically-adjusted linear models for each contaminant or pollutant class. Classes were modelled separately, in order to reduce model complexity and allow interactions among explanatory variables for each contaminant or pollutant class to be thoroughly explored. 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 dataset 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. The resultant response variable in these models was effect size, while the explanatory variables were level of the relevant stressor (e.g. contaminant concentration or pollutant level for each treatment), exposure period, number of replicates, group size, exposure type (acute, acclimated, repeated, developmental, or uncontrolled), and metric (group cohesion or sociability). For studies of wild populations, i.e. where exposure period and group size were not known, 100 days and group size of 10 individuals (arbitrarily chosen values corresponding to long-term exposure and high group size relative to lab studies) were used to allow inclusion of wild studies in models. The interaction effect between contaminant concentration or pollutant level and metric was also included where multiple concentrations were present within each metric. In the case of light pollution, an interaction between the form of light exposure and treatment was included in order to separate effects of luminance from different wavelengths. While metric was likely somewhat collinear with group size, interactions between these variables were not included as the majority of variables had only one value for sociability trial group size (one). Specimen, referring to different treatments both within and among papers utilising the same species, was also included as a random effect variable to account for the effects of different trials, both within and across studies, using the same species. Species was also included as a random effect variable, as is required to quantify phylogenetic effects in MCMCglmm models. Sex of fish(es) used in each trial was also included as a random effect variable. Multi-stressor interactions were not modelled due to the small number of studies that investigated stressor combinations. Lambda (λ) value, and 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 ggplot2 (Wickham, 2016), ggraph (Pedersen, 2022), and ggtree (Yu et al., 2017) packages in R.

Supplementary Materials: Chapters 4 & 5

Supplementary Table 4.1A. Correlational matrix of individual traits measured in individual risk-taking behaviour and sociability temperature ramp trials. Values above the diagonal are p values; values below the diagonal are Pearson's correlation coefficients. Significant correlations at $p < 0.05$ are shown in bold; correlations with weak evidence at $p < 0.1$ are shown in italics.

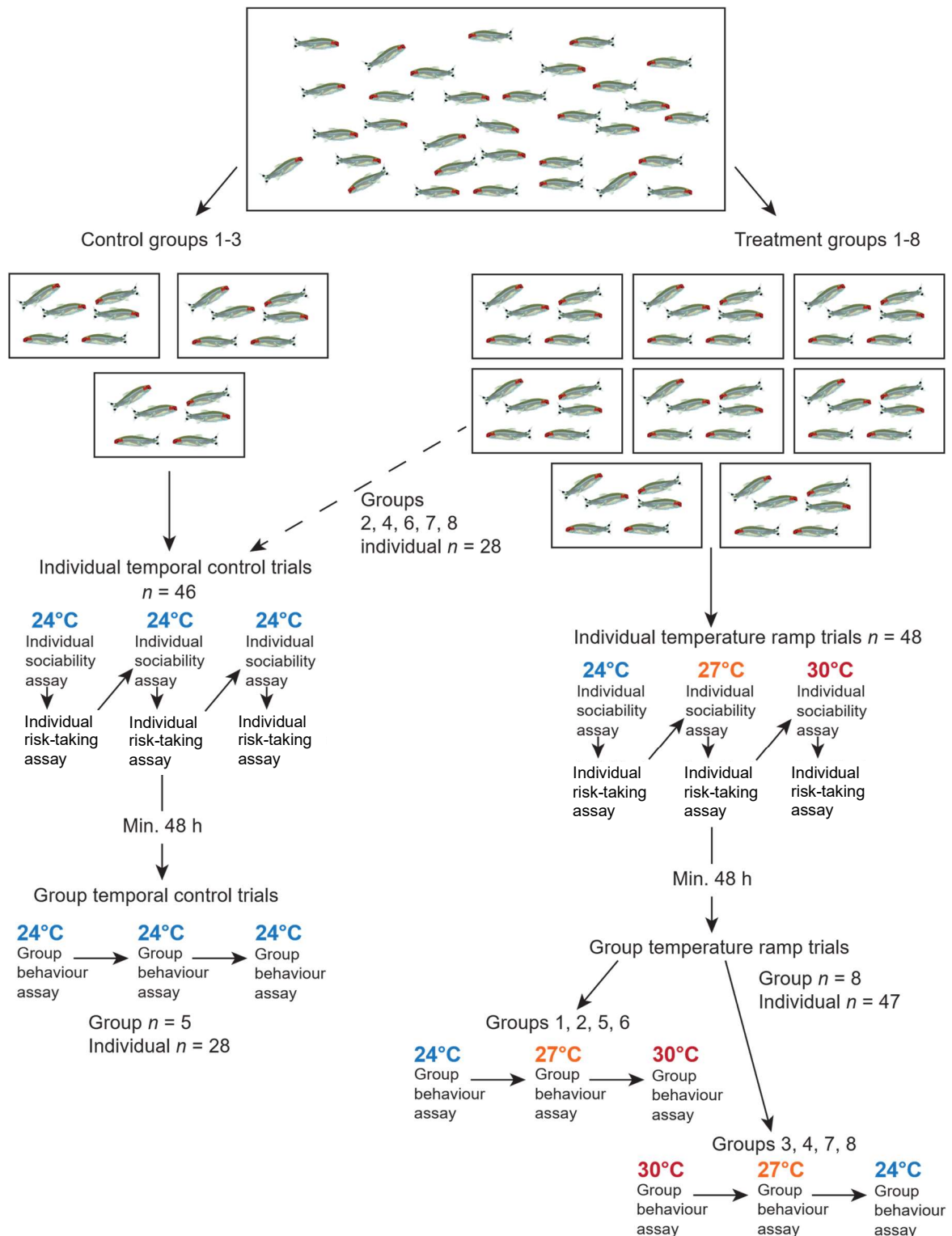
	MDNS	Activity (risk-taking)	Activity (sociability)	DCS	SL
MDNS		0.393	0.022	<i>0.055</i>	0.861
Activity (risk-taking)	0.073		<0.001	0.039	<i>0.064</i>
Activity (sociability)	0.194	0.445		<0.001	0.015
DCS	<i>-0.162</i>	-0.174	-0.448		0.256
SL	-0.015	<i>0.157</i>	-0.205	0.097	

MDNS = mean distance to nearest shelter, SL = standard length.

Supplementary Table 4.1B. Correlational matrix of individual traits measured in group temperature ramp trials. Values above the diagonal are p values; values below the diagonal are Pearson's correlation coefficients. Correlations with moderate to strong evidence at $p < 0.05$ are shown in bold; correlations with weak evidence at $p < 0.1$ are shown in italics.

	MDCS	NND	TA	Heading	Bearing	Distance along	Speed	SL
MDCS		<0.001	0.663	0.418	0.176	<i>0.083</i>	0.018	0.204
NND	0.816		0.153	0.695	< 0.001	0.261	0.004	0.002
TA	0.037	0.121		<0.001	0.169	0.289	<0.001	0.146
Heading	0.069	-0.033	0.678		0.022	0.335	<0.001	0.509
Bearing	0.115	0.576	0.117	-0.193		0.982	0.019	0.109
Distance along	<i>0.147</i>	0.096	-0.090	-0.082	0.002		0.001	0.274
Speed	0.200	0.240	-0.713	-0.819	0.199	0.270		0.207
SL	0.108	0.257	0.124	0.056	0.136	0.093	0.107	

MDCS = mean distance to centroid of the shoal; NND = nearest neighbour distance; TA = turning angle; Distance = mean distance along group motion; SL = standard length.



Supplementary Figure 4.1. Summary of experimental design and number of individual and group replicates per treatment. Fish were initially held in two large holding tanks (one shown) and randomly allocated to groups. Treatment groups 2, 4, 6, 7, and 8 were used in both temperature ramp and temporal control trials, in that order. Treatment groups 1, 3, and 5 were exposed to temperature ramp trials only, while control groups were exposed to temporal control trials only. Control groups were excluded from group trial analyses due to failure to resume normal behaviour.

Supplementary Table 4.2/5.3. Effects of time (trial number) on behavioural metrics measured in group trials. Data from temporal control trials.

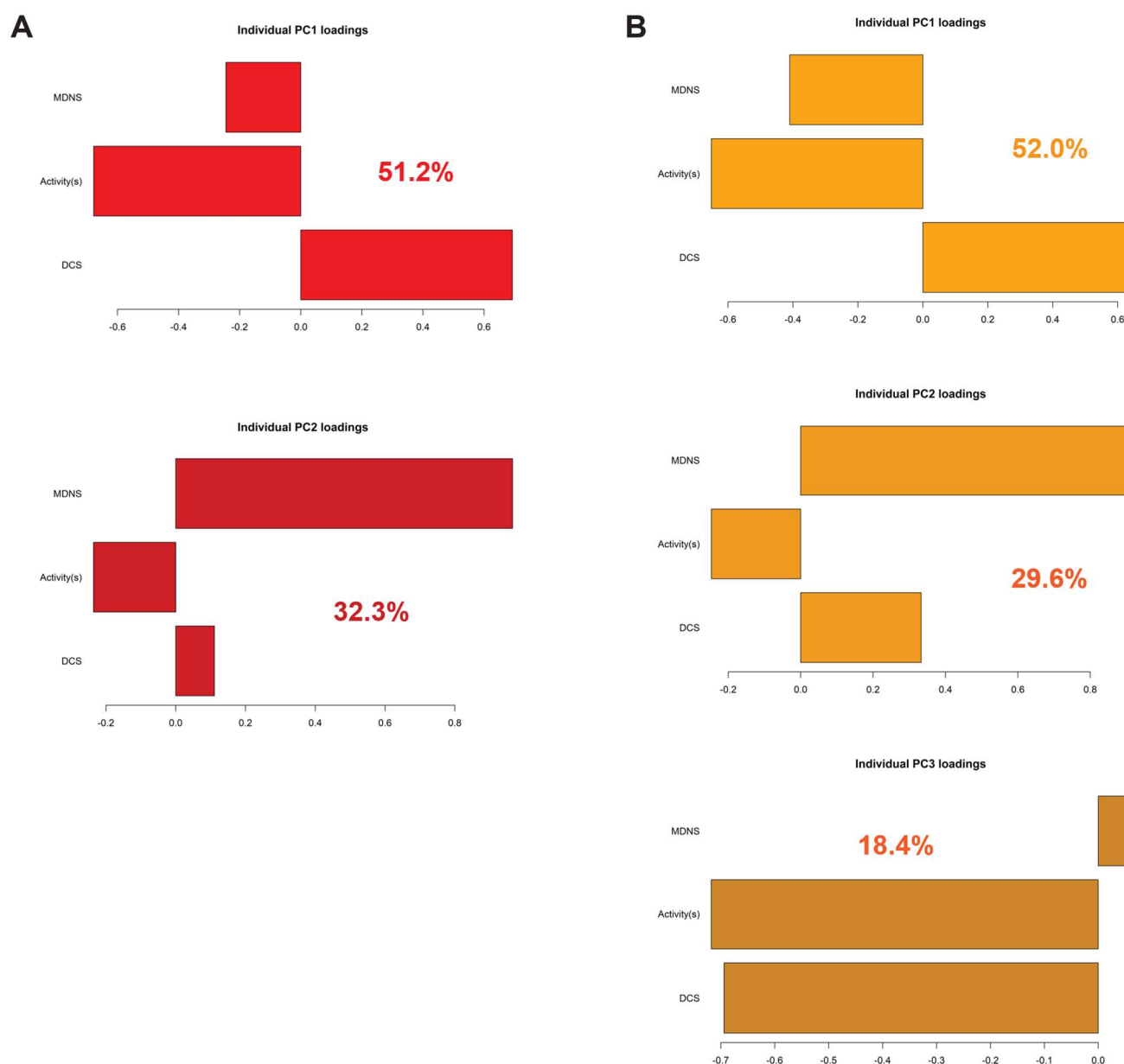
Response	Explanatory	Estimate	Standard error	z	p
Distance along	Intercept	0.070	0.055	1.263	0.206
	Trial number	-0.009	0.023	-0.389	0.697
MDCS	Intercept	3.463	0.298	11.61	< 0.001
	Trial number	0.683	0.070	9.764	< 0.001***
TA	Intercept	2.041	0.161	12.71	< 0.001
	Trial number	0.219	0.033	6.668	< 0.001***
Speed	Intercept	6.124	0.407	15.03	< 0.001
	Trial number	-0.615	0.062	-9.844	< 0.001***
Bearing	Intercept	1.925	0.127	15.19	< 0.001
	Trial number	0.0009	0.053	0.018	0.986
Heading difference	Intercept	48.58	3.001	16.19	< 0.001
	Trial number	7.597	0.474	16.01	< 0.001***
NND	Intercept	-0.496	0.117	-4.234	< 0.001
	Trial number	0.229	0.026	8.827	< 0.001***
Group speed	Intercept	1.655	0.068	24.37	< 0.001
	Trial number	-0.147	0.023	-6.499	< 0.001***
Group polarisation	Intercept	-0.345	0.044	-7.859	< 0.001
	Trial number	-0.125	0.018	-6.979	< 0.001***

MDCS = mean distance to centre of shoal; TA = turning angle; NND = nearest neighbour distance.

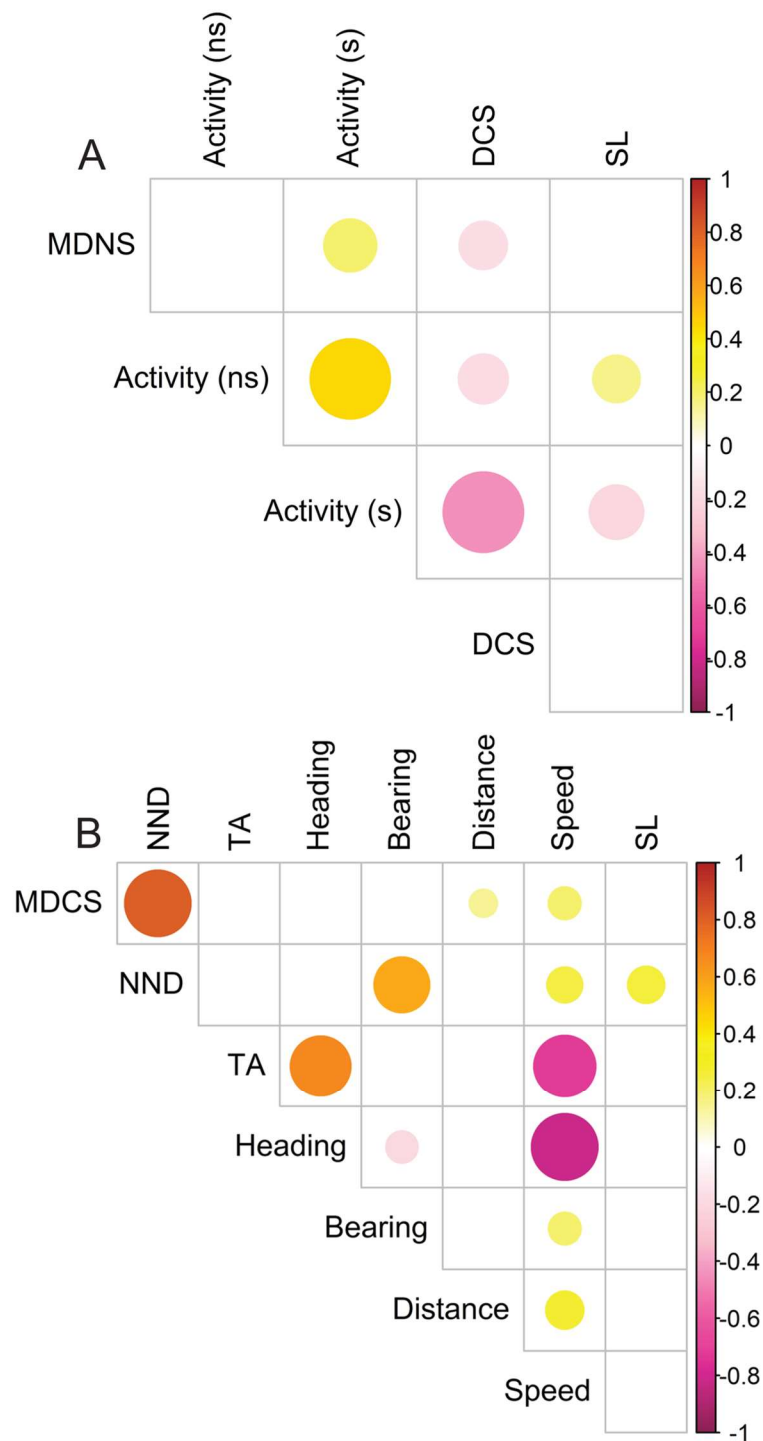
Supplementary Table 4.3/5.1. Size distribution of fish within groups.

Group	Mean standard length (mm)	SE standard length (mm)	Mean mass (g)	SE mass (g)
Treatment group 1	27.07	1.069	0.552	0.109
Treatment group 2	29.38	1.279	0.808	0.106
Treatment group 3	28.59	0.740	0.514	0.057
Treatment group 4	27.32	0.855	0.481	0.087
Treatment group 5	27.60	0.715	0.414	0.042
Treatment group 6	27.40	0.746	0.445	0.044
Treatment group 7	28.07	1.417	0.482	0.068
Treatment group 8	28.98	0.721	0.528	0.037
Control group 1	27.35	1.134	0.492	0.057
Control group 2	28.48	1.427	0.496	0.077
Control group 3	31.67	0.850	0.665	0.055

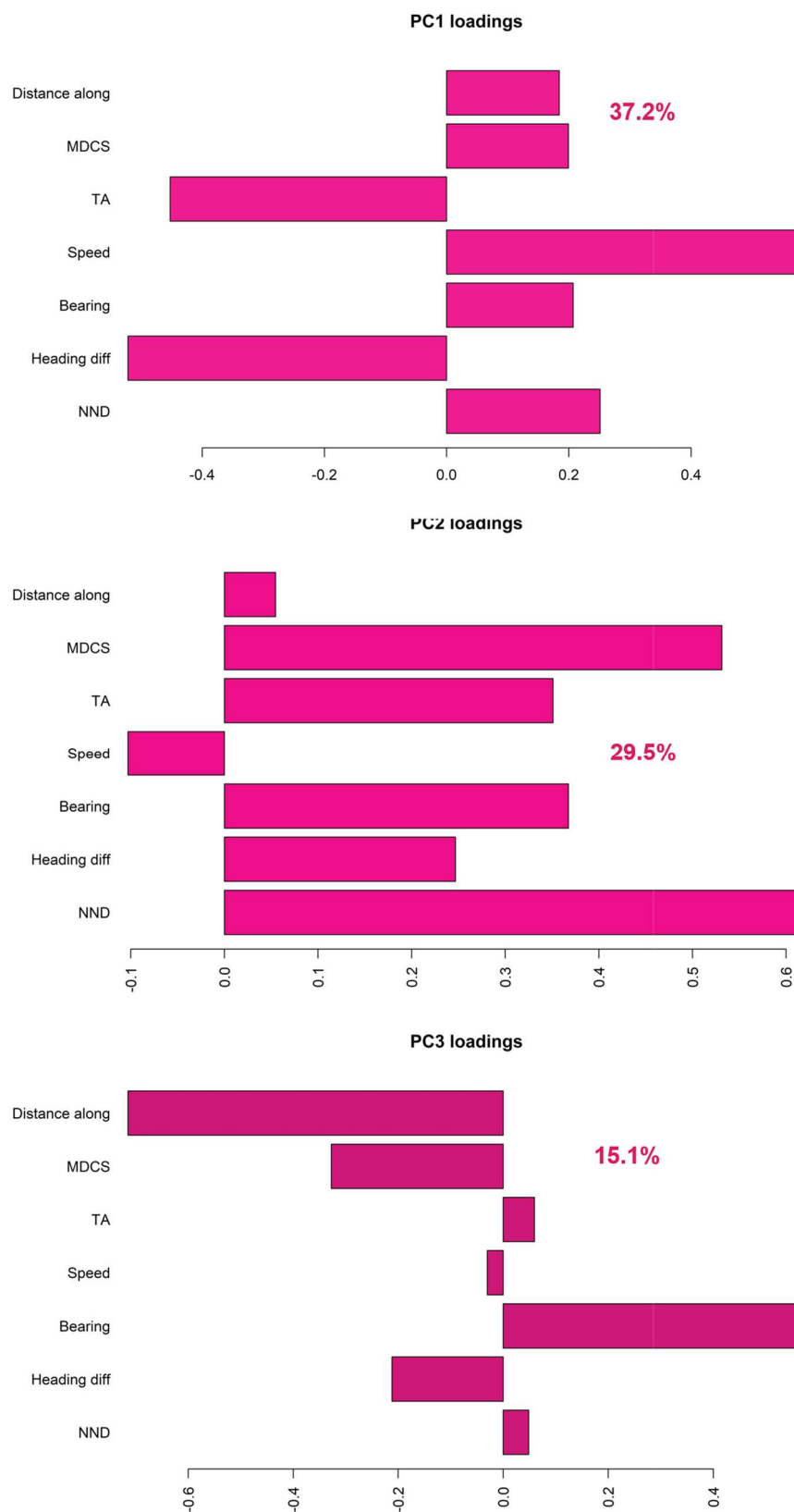
SE = standard error.



Supplementary Figure 4.2. Principal components of metrics measured in individual behavioural trials constructed using A. Data from both control and temperature ramp trials and B. Data from temperature ramp trials only. DCS = distance to conspecific shoal, MDNS = mean distance to nearest shelter.



Supplementary Figure 4.3. Correlations among traits observed in A. individual behavioural trials and B. group behavioural trials. Data from temperature ramp trials. Blank squares indicate non-significant correlations ($p > 0.1$). Larger, more opaque circles indicate stronger correlations. MDNS = mean distance to nearest shelter. Activity (ns) = activity in risk-taking behaviour trials. Activity (s) = activity in sociability trials. DCS = distance to conspecific shoal. NND = nearest neighbour distance. TA = turning angle. MDCS = mean distance to centre of shoal.



Supplementary Figure 4.4. Principal components explaining 82% of variance in metrics measured at the individual level in group temperature ramp trials. MDCS = mean distance to the centre of the shoal. TA = turning angle i.e., degree of change in direction of a fish from time t-2 to time t. NND = nearest neighbour distance.

Supplementary Table 5.2A. Correlational matrix of individual traits measured in individual risk-taking behaviour and sociability hypoxia ramp trials. Correlations with moderate to strong evidence at $p < 0.05$ are shown in bold

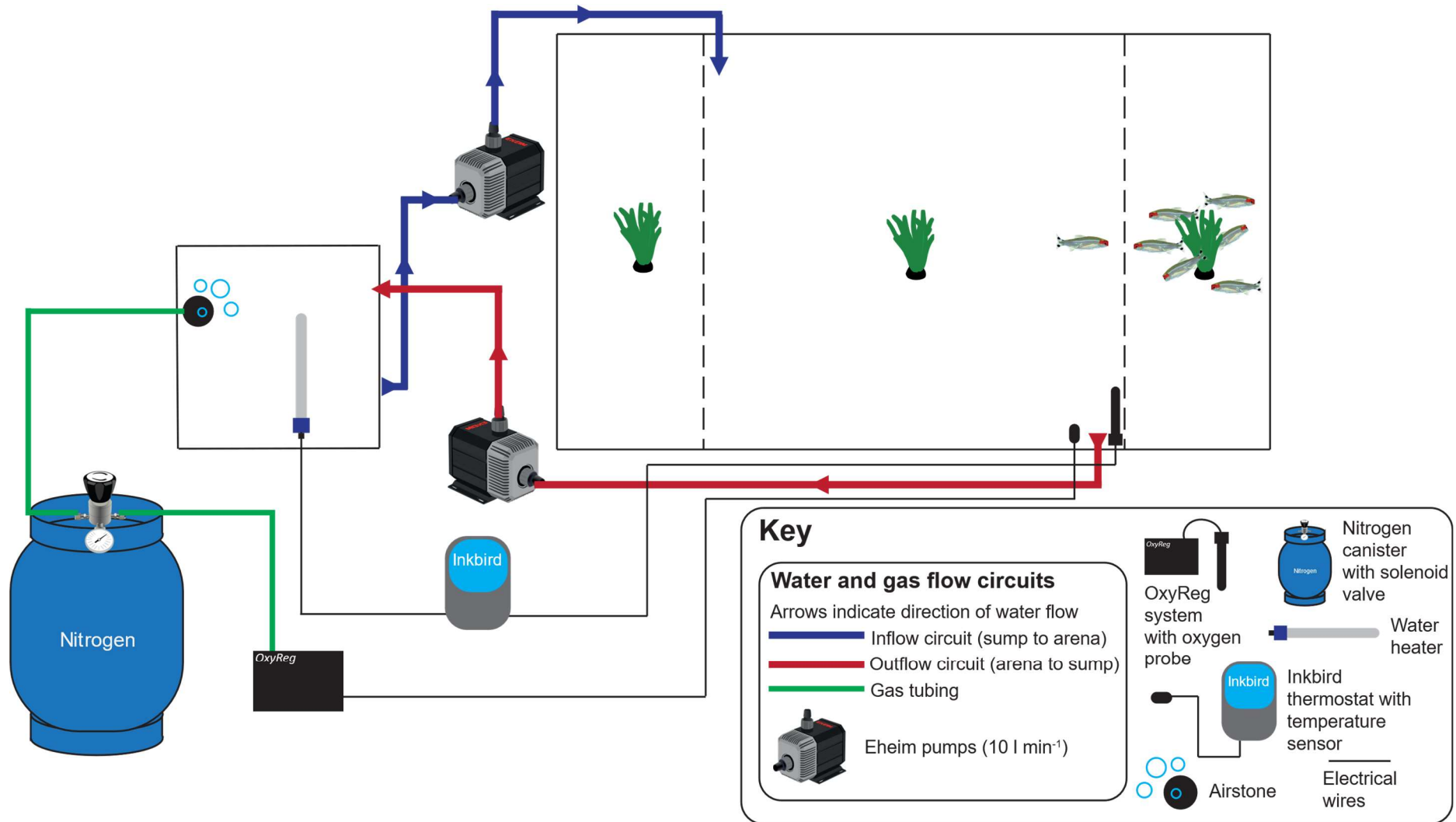
	MDNS	Activity _{ns}	Activity _s	DCS	SL
MDNS		0.114	0.111	0.045	0.926
Activity _{ns}	0.138		< 0.001	0.038	0.657
Activity _s	0.139	0.432		< 0.001	0.046
DCS	-0.175	-0.181	-0.438		0.540
SL	-0.008	0.039	-0.174	-0.054	

Activity_{ns} = speed in individual risk-taking behaviour trials; Activity_s = speed in individual sociability trials; SL = standard length.

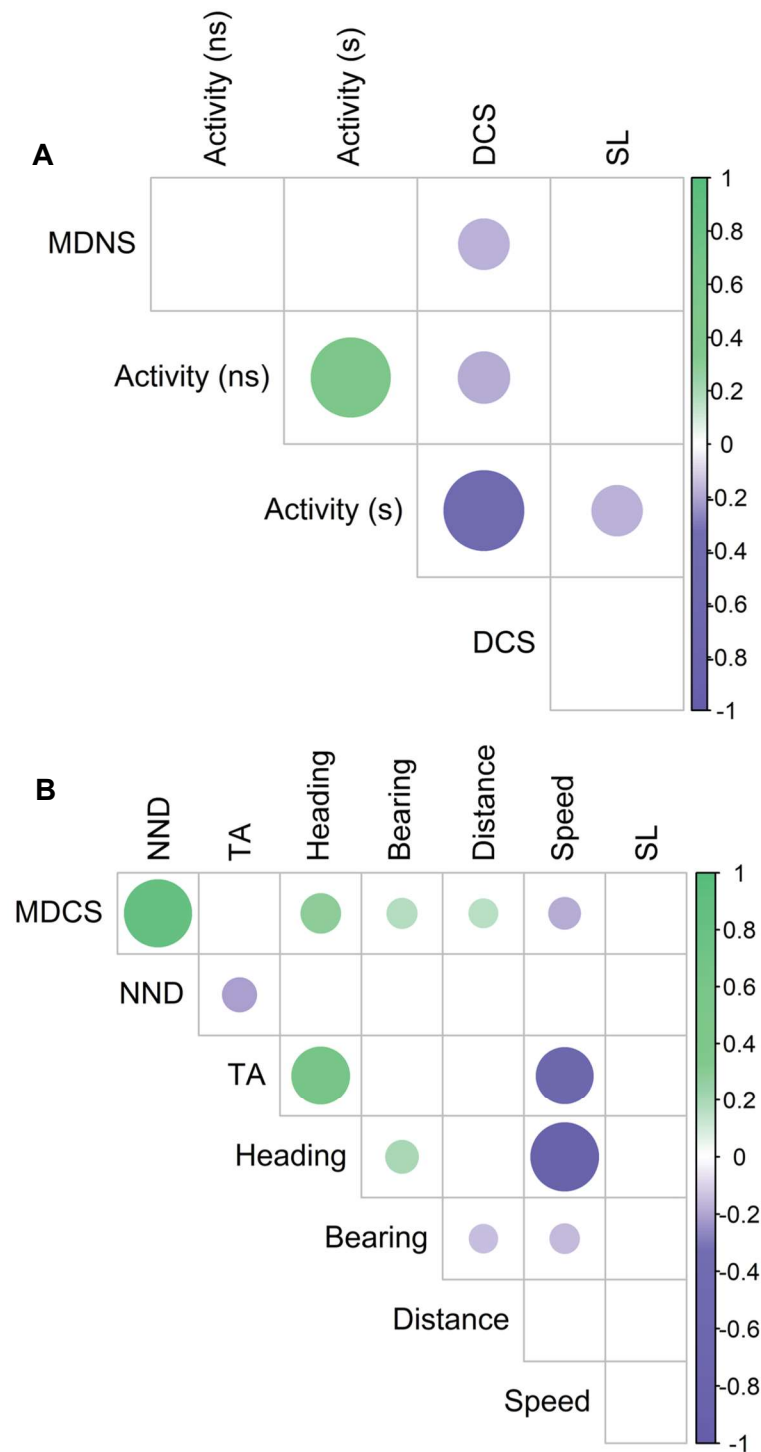
Supplementary Table 5.2B. Correlational matrix of individual traits measured in group hypoxia ramp trials. Correlations with moderate to strong evidence at $p < 0.05$ are shown in bold; correlations with weak evidence at $p < 0.1$ are shown in *italics*

	MDCS	NND	TA	Heading	Bearing	Distance	Speed	SL
MDCS		< 0.001	0.576	< 0.001	<i>0.058</i>	<i>0.082</i>	0.034	0.616
NND	0.829		0.015	0.202	0.218	0.122	0.582	0.612
TA	-0.049	-0.211		< 0.001	0.552	0.276	< 0.001	0.248
Heading	0.285	0.112	0.612		0.026	0.631	< 0.001	0.464
Bearing	<i>0.165</i>	0.108	0.052	0.194		<i>0.095</i>	<i>0.073</i>	0.530
Distance	<i>0.152</i>	0.135	-0.095	-0.042	<i>-0.146</i>		0.153	0.281
Speed	-0.184	-0.048	-0.594	-0.844	<i>-0.157</i>	0.125		0.543
SL	0.044	0.044	0.101	0.064	0.055	0.094	-0.053	

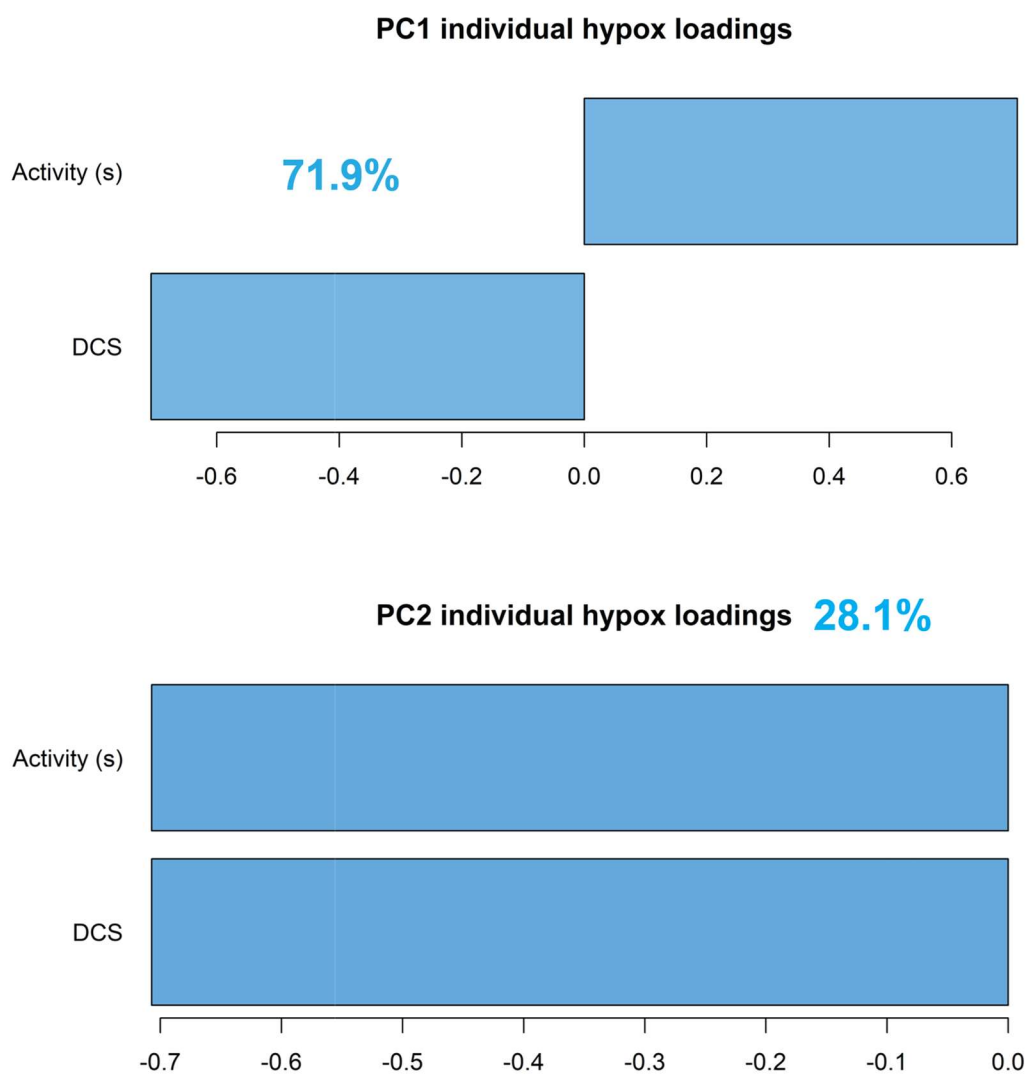
MDCS = mean distance to centroid of the shoal; NND = nearest neighbour distance; TA = turning angle; Distance = mean distance along group motion; SL = standard length.



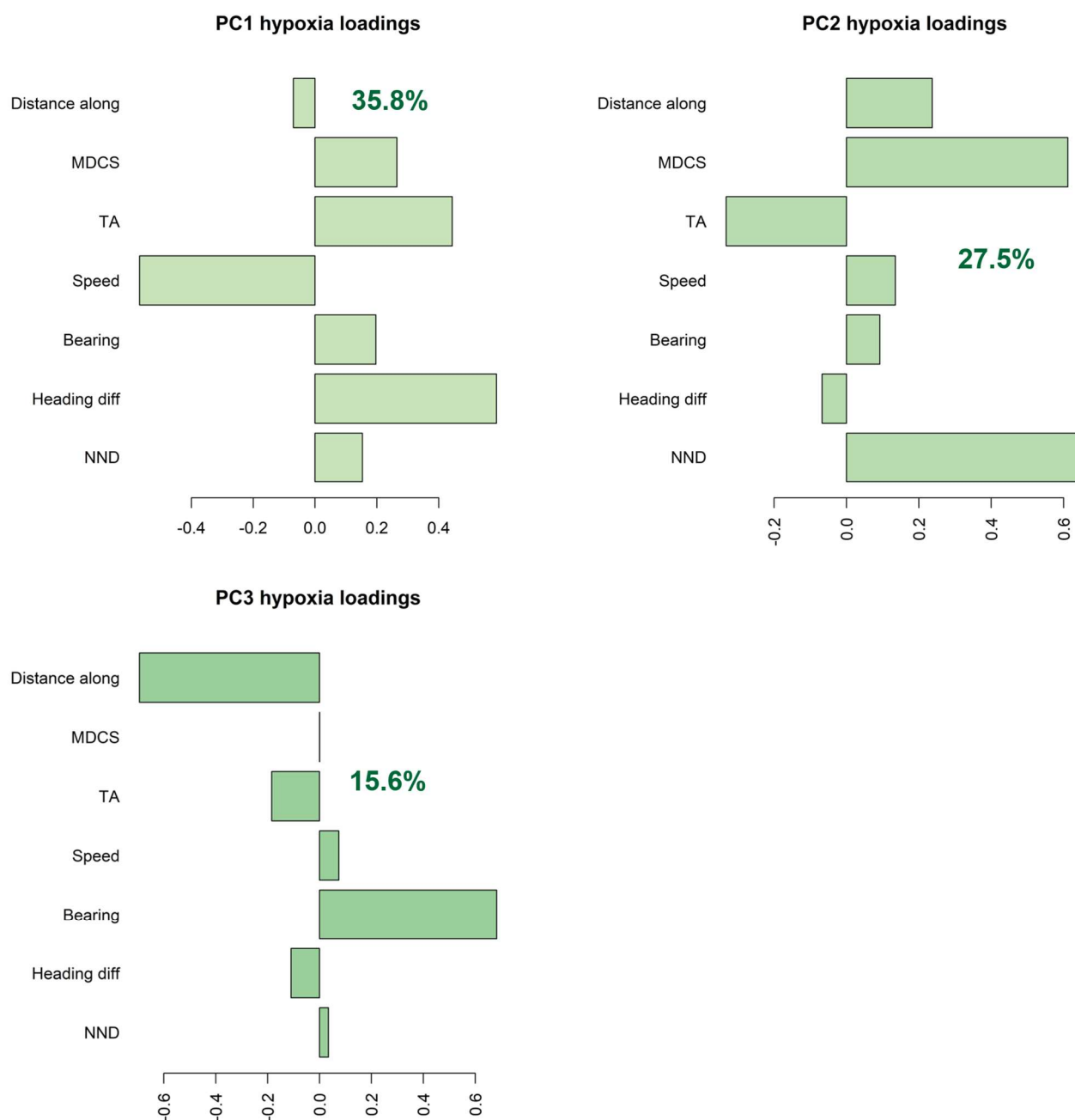
Supplementary Figure 5.1. Diagram showing setup of behavioural arenas, temperature-regulated water sump, and nitrogen canister used to induce hypoxia. Temperature and oxygen sensors were positioned in the corner of the chamber so as not to obscure the view of the stimulus shoal. Position of the stimulus shoal relative to the inflow and outflow of water was alternated. Water inflow was through a standpipe placed in the corner opposite the outflow pipe and temperature and oxygen sensors, while outflow was through a hole drilled in the side of the arena.



Supplementary Figure 5.2. Correlations among traits observed in A. individual behavioural trials and B. group behavioural trials. Data from hypoxia ramp trials. Increasing size and opacity of circles indicates increasing strength of correlations. Blank squares indicate no evidence for a correlation ($p > 0.1$). MDNS = mean distance to nearest shelter. DCS = distance to conspecific shoal. MDCS = mean distance to centre of shoal. NND = nearest neighbour distance. TA = turning angle. SL = standard length.



Supplementary Figure 5.3. Principal components explaining 100% of variance in metrics measured in individual sociability trials. DCS = distance to conspecific shoal.



Supplementary Figure 5.4. Principal components explaining 78.9% of variance in metrics measured for individual fish in group trials. MDCS = mean distance to the centre of the shoal, TA = turning angle i.e., degree of change in direction of a fish from time t-2 to time t, NND = nearest neighbour distance.

Supplementary methods

Thigmotaxis (T) **Supplementary Equation 4.1:**

$$T_{beta} = \frac{T}{101}$$

Activity (cm s⁻¹) **Supplementary Equation 4.2:**

$$Activity_{beta} = \frac{Activity}{13}$$

< 0.3 cm s⁻¹ adjusted to zero to account for low-value inflation

Supplementary Equation 5.1:

$$Thigmotaxis_{adj} = \frac{Thigmotaxis (\%)}{100}$$

Values at or above 1 were adjusted to 0.9999 in line with the requirements of beta distributions.

Supplementary Equation 5.2:

$$Activity_{adj} = \frac{Activity_{ns}}{14}$$

Values of < 0.3 cm s⁻¹ were adjusted to zero prior to transformation

Supplementary Equation 5.3:

$$Group\ PC1_{adj} = \frac{Group\ PC1 + 4}{10}$$

Individual-level traits in temporal control trials were modelled according to

Supplementary model 4.1/5.1:

MDCS ~ Trial number + (1|Group ID/Fish ID) + (1|Group size)

Group-level traits in temporal control trials were modelled according to **Supplementary model 4.2/5.2:**

Group speed ~ Trial number + (1|Group ID) + (1|Group size)

Data from control groups (*n* = 3 groups) was excluded due to failure to resume normal behaviour in group trials (reason unknown), therefore individual *n* = 28 and group *n* = 5.

Metrics of individual behaviour in group trials

Interindividual distances

1. Mean nearest neighbour distance (NND), i.e., the distance between an individual and its closest neighbour, in cm.
2. Mean distance of an individual to the centroid of the shoal (MDCS), in cm.

Activity

1. Median speed of each individual, in cm s^{-1} . Median speed (and turning angle, rescaled bearing, and heading difference; see below) were only calculated when individual speed was $\geq 1 \text{ cm s}^{-1}$, indicating that fish were swimming. This minimum value was based on the frequency distribution of speeds, where the mode at 1 cm s^{-1} indicated that this represents the minimum speed of swimming.

Polarisation

1. Median turning angle (TA) of each individual. TA was defined as the change in direction of a fish between frames, in degrees.
2. Mean rescaled bearing to the nearest neighbour, i.e. the mean angular direction of the individual's nearest neighbour, in degrees. As the (unscaled) bearing angle could range from 0 - 180° , calculating a mean angle for an individual with a neighbour directly in front (0°) for half the trial and directly behind (180°) for the other half would result in a mean of 90° i.e., alongside the nearest neighbour, which would be unrepresentative. The bearing was therefore rescaled so that the nearest neighbour being directly in front of or directly behind an individual were both recorded as a bearing of 0° , while the nearest neighbour being directly alongside was recorded as 90° (MacGregor and Ioannou, 2023). An increase in mean rescaled bearing therefore indicated spatial positioning of nearest neighbours more alongside the individual.
3. Mean heading difference from nearest neighbour. This was defined as the difference in direction of travel between the individual and its nearest neighbour, in degrees.

Position in group

1. Mean normalised distance along the group's direction of motion. This was only calculated from time points where group polarisation was greater than 0.3, i.e., when fish were swimming in approximately the same direction. Distance along the group's direction of motion for each individual at each time point was calculated as the relative position of each individual to the movement direction of the group centroid. This was then normalised to account for the variation in spacing between individuals over time, and was calculated by assigning the frontmost fish at a given time point a distance of 1, and the rearmost fish a distance of zero. The position of the other individuals along the group's direction of motion was calculated as a proportion of the distance between the frontmost and rearmost fish.

Metrics of group-level behaviour

1. Median group speed in cm s^{-1} , i.e. the distance the group centroid moved between frames. This was calculated from the position of the group centroid at time t and time $t-1$.

2. Mean group polarisation, i.e. the tendency of fish in the shoal to face and swim in the same direction. Mean group polarisation was calculated only from time points when group speed was $\geq 1 \text{ cm s}^{-1}$, i.e. when the group was swimming together and polarisation could be calculated reliably. Polarisation ranged from 0-1, where 0 indicates no individuals facing or swimming in the same direction, and 1 indicates all individuals swimming and facing in the same direction.

Supplementary Material: Chapter 6

Supplementary Table 6.1. Light measurements taken at control and ALAN-exposed sites from which *Dascyllus trimaculatus* were collected. Lunar cycle indicates the date on which measurements were taken relative to the full moon.

Site	Treatment	Anemone/area	Lunar cycle	Light level (lux)
1	ALAN	2322	Full moon + 1d	13.35 ± 0.153
1	ALAN	2328	Full moon	32.96 ± 0.500
1	ALAN	2347	Full moon + 1d	5.248 ± 0.068
1	ALAN	408	Full moon + 1d	12.05 ± 0.176
1	ALAN	769	Full moon – 1d	4.987 ± 0.043
1	ALAN	797	Full moon – 1d	7.249 ± 0.135
1	ALAN	909	Full moon + 4d	5.943 ± 0.058
1	ALAN	Pillar	Full moon + 4d	1.458 ± 0.018
1	Control	2314	Full moon + 4d	0.004 ± 0.002
1	Control	2327	Full moon + 1d	0.003 ± 0.002
1	Control	908	Full moon – 1d	0.010 ± 0.003
2	ALAN	56	Full moon	2.282 ± 0.048
2	ALAN	807	Full moon – 1d	2.127 ± 0.038
2	ALAN	910	Full moon	2.253 ± 0.043
2	ALAN	911	Full moon – 1d	1.075 ± 0.023
2	ALAN	912	Full moon	6.352 ± 0.118
2	ALAN	913	Full moon	12.55 ± 0.213
2	ALAN	914	Full moon – 1d	3.282 ± 0.059
2	Control	59	Full moon	0.001 ± 0.0004
2	Control	799	Full moon – 1d	0.004 ± 0.002
3	ALAN	B	Full moon – 2d	21.21 ± 0.707
3	Control	C	Full moon – 2d	0.013 ± 0.005
3	Control	D	Full moon + 8d	0.003 ± 0.001

Supplementary Table 6.2. Welch's t statistics comparing mass and total length of *Dascyllus trimaculatus* raised under control or ALAN conditions.

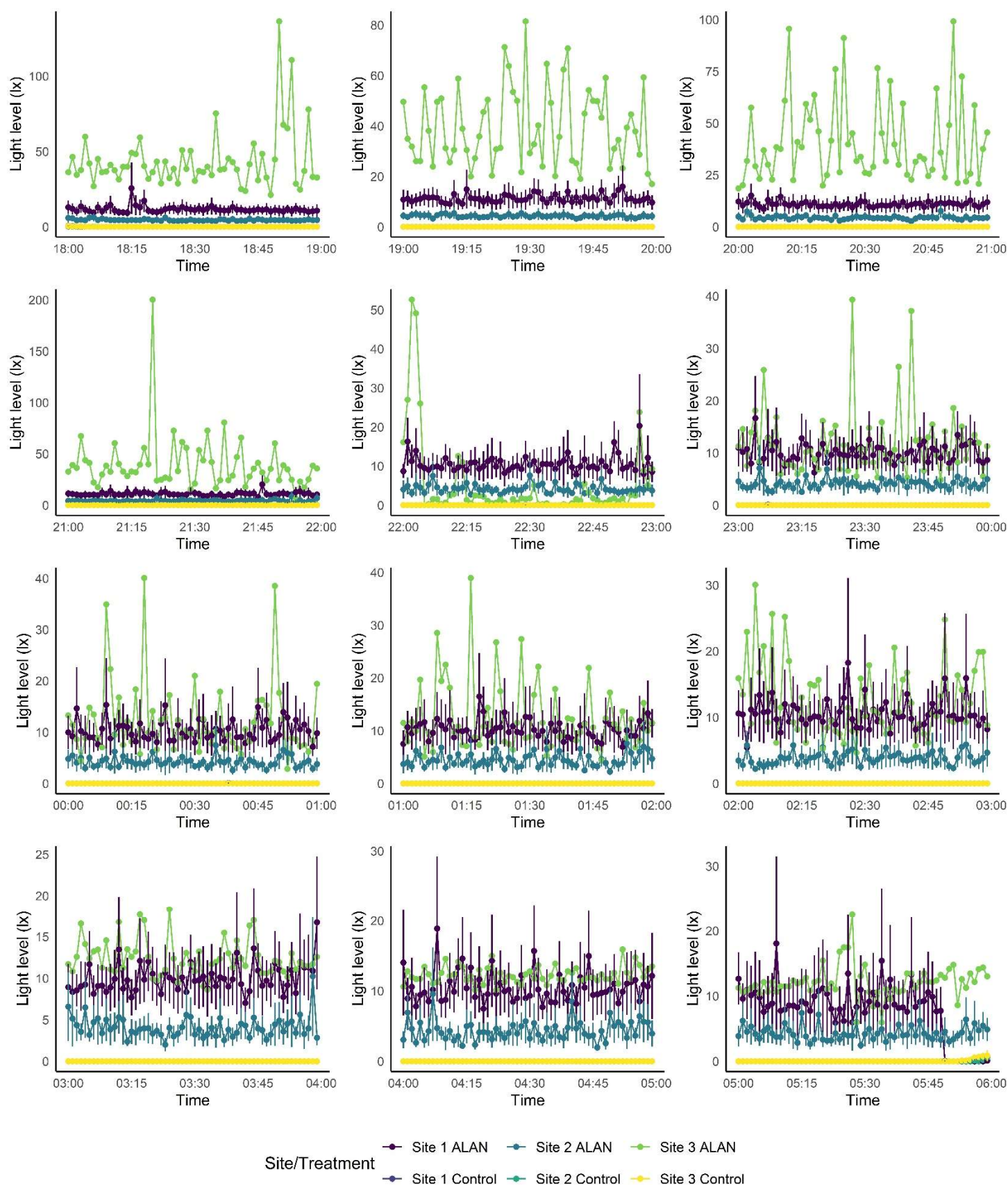
Variable	Treatment	Welch's t statistic	Df	p value
Mass (g)	ALAN	0.287	15.7	0.778
Total length (mm)	ALAN	-0.442	16.3	0.665

Supplementary Table 6.3. Effects of side and size of stimulus shoal on behaviour of *Dascyllus trimaculatus* in sociability trials. Reference level for stimulus shoal side is left.

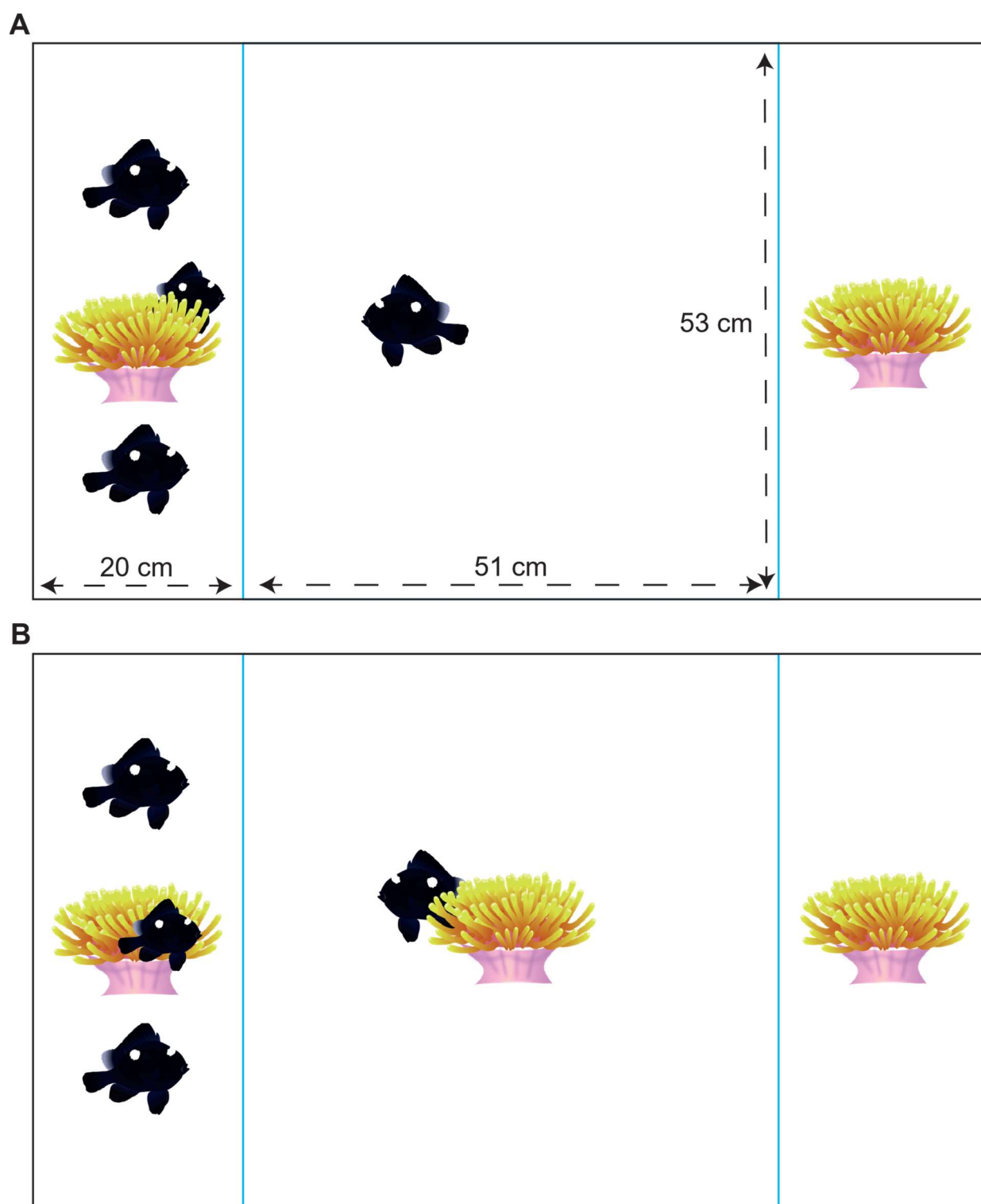
<i>Model response variable</i>	Explanatory variable	Estimate	Standard error	z value	p value
<i>Distance to a conspecific shoal (cm)</i>					
	Intercept	1.740	0.528	3.295	< 0.001
	Stimulus shoal size	0.044	0.116	0.384	0.701
	Stimulus shoal side (Right)	-0.284	0.206	-1.379	0.168
<i>Percentage time spent moving</i>					
	Intercept	0.750	0.126	5.939	< 0.001
	Stimulus shoal size	-0.012	0.032	-0.358	0.720
	Stimulus shoal side (Right)	-0.053	0.061	-0.874	0.382

Supplementary Table 6.4. Correlations among behavioural traits observed in *Dascyllus trimaculatus* in emergence and sociability trials. Pearson's correlation coefficient is shown above the diagonal; p values are shown below the diagonal. Correlations with evidence at $p < 0.1$ are shown in bold. Sociability_s = distance to conspecific shoal in sociability trials, MDS = distance to shelter (anemone) after first emergence in emergence trials, sociability_e = distance to conspecific shoal in emergence trials, activity_s = mean speed of movement in sociability trials, activity_e = mean speed of movement in emergence trials.

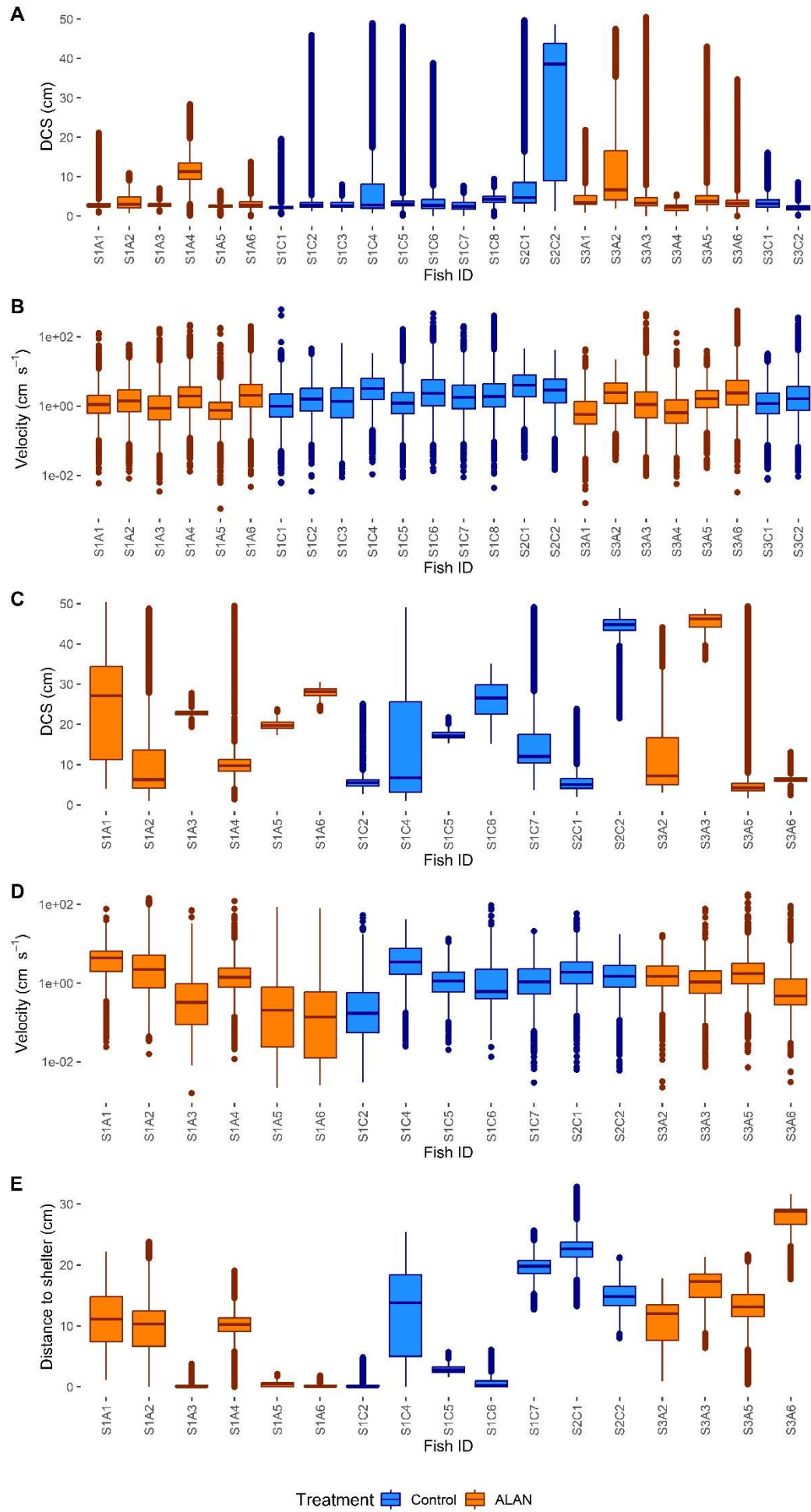
	Time to emerge (s)	Activity _s (% time moving)	Mean sociability _s	MDS	Mean sociability _e	Activity _e (% time moving)
Time to emerge (s)		-0.183	-0.303	-0.662	0.238	-0.549
Activity _s (% time moving)	0.080		0.451	0.479	-0.278	0.429
Mean sociability _s	0.117	0.030		0.217	0.348	0.389
MDS	0.004	0.052	0.403		-0.130	0.484
Mean sociability _e	0.358	0.280	0.171	0.618		-0.048
Activity _e (% time moving)	0.023	0.086	0.123	0.049	0.856	



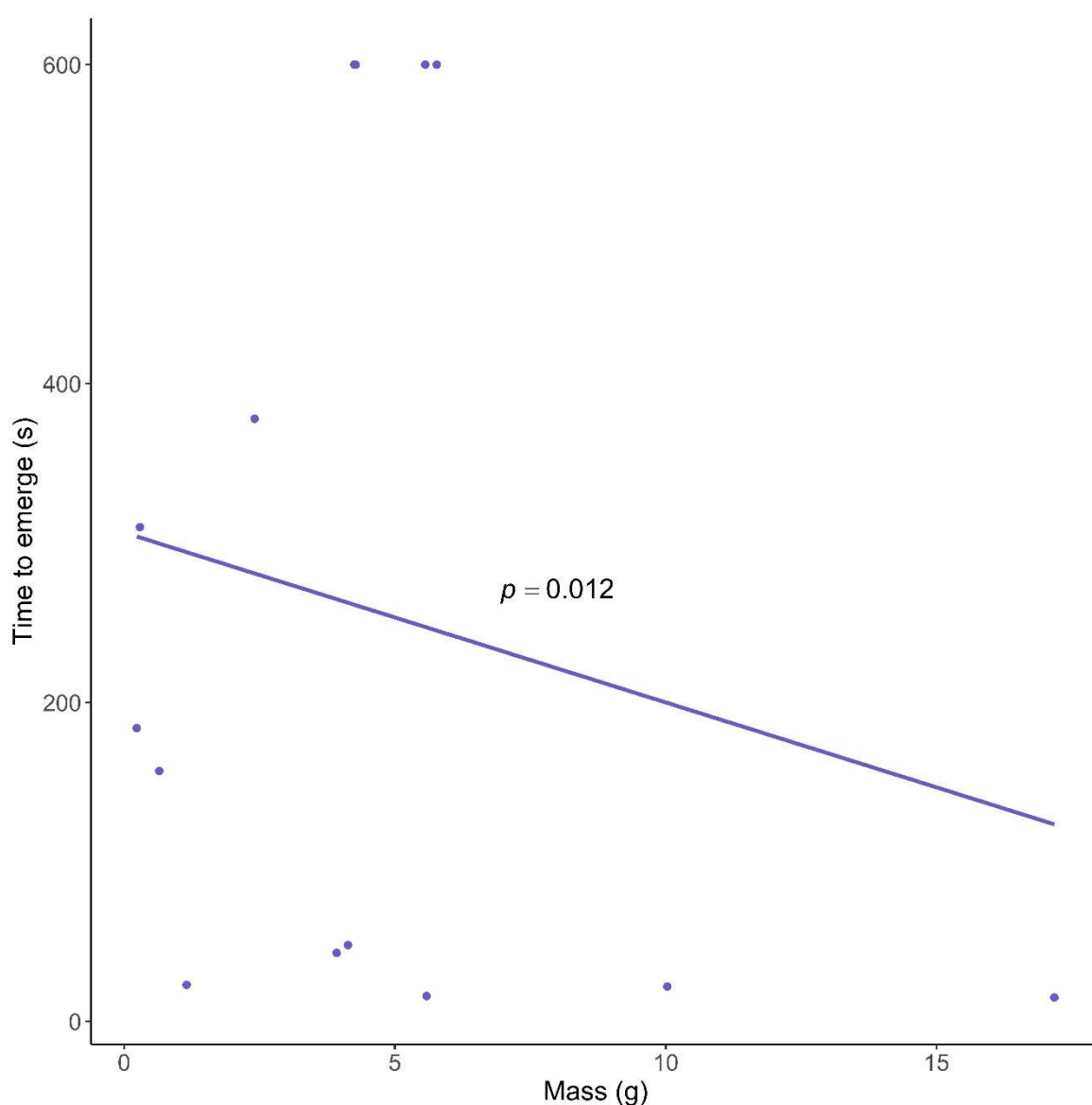
Supplementary Figure 6.1. Light levels across sites from 6pm (18:00) to 6am (06:00) under artificial light at night (ALAN) and control light conditions.



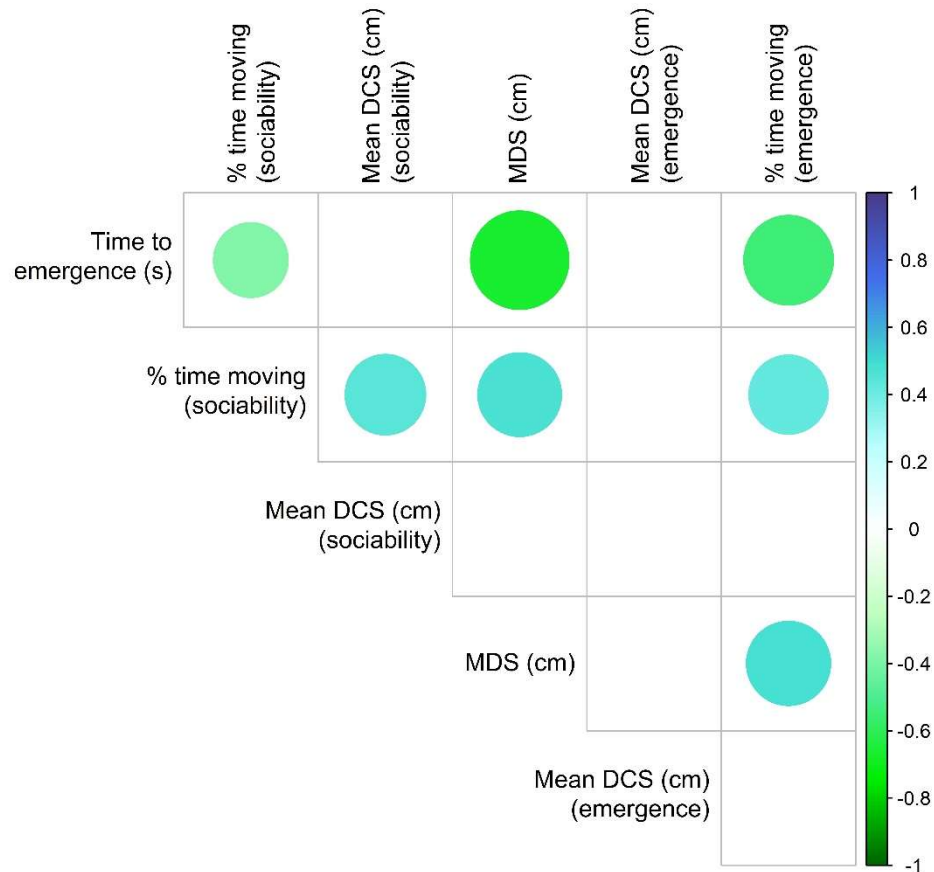
Supplementary Figure 6.2. Schematic showing tank setup during A. sociability trials and B. emergence behaviour tests. Blue lines indicate transparent Perspex dividers.



Supplementary Figure 6.3. Raw data distribution per individual fish for A. Distance to the conspecific shoal (DCS) in sociability trials, B. Speed of movement (velocity) in sociability trials, C. Distance to the conspecific shoal (DCS) in emergence trials, D. Speed of movement (velocity) in emergence trials, and E. Distance to anemone after first emergence in emergence trials. Notation of individual IDs is in the format site number-treatment-individual i.e., S1A1 indicates fish 1 collected at Site 1 from an artificial light at night-exposed anemone; S2C2 indicates fish 2 collected at Site 2 from an anemone exposed to control lighting. Note that velocity graphs are plotted on a log scale.



Supplementary Figure 6.4. Relationship between time to emerge from an anemone following a chase stimulus and fish mass.



Supplementary Figure 6.5. Correlations among traits observed in *Dascyllus trimaculatus*. Scales indicate r values. Increasing size and opacity of circles indicates increasing evidence for correlation based on p values. Blank squares indicate no evidence for a correlation ($p > 0.1$). DCS = distance to conspecific shoal. MDS = mean distance to shelter (anemone).

Supplementary methods

Supplementary Equation 6.1:

$$\text{Mean distance to anemone}_{\text{beta}} = \frac{\text{Mean distance to anemone}}{28}$$

Where “mean distance to anemone” refers to the distance of the focal fish to the anemone shelter during emergence trials, and “mean distance to anemone_{beta}” refers to the transformed values of the variable subsequently used in the model.

Reference list

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