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REVIEW PAPER

# An updated review of cold shock and cold stress in fish

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## Abstract

Temperature is critical in regulating virtually all biological functions in fish. Low temperature stress (cold shock/stress) is an often-overlooked challenge that many fish face as a result of both natural events and anthropogenic activities. In this study, we present an updated review of the cold shock literature based on a comprehensive literature search, following an initial review on the subject by M.R. Donaldson and colleagues, published in a 2008 volume of this journal. We focus on how knowledge on cold shock and fish has evolved over the past decade, describing advances in the understanding of the generalized stress response in fish under cold stress, what metrics may be used to quantify cold stress and what knowledge gaps remain to be addressed in future research. We also describe the relevance of cold shock as it pertains to environmental managers, policymakers and industry professionals, including practical applications of cold shock. Although substantial progress has been made in addressing some of the knowledge gaps identified a decade ago, other topics (*e.g.*, population-level effects and interactions between primary, secondary and tertiary stress responses) have received little or no attention despite their significance to fish biology and thermal stress. Approaches using combinations of primary, secondary and tertiary stress responses are crucial as a research priority to better understand the mechanisms underlying cold shock responses, from short-term physiological changes to individual- and population-level effects, thereby providing researchers with better means of quantifying cold shock in laboratory and field settings.

**KEYWORDS**
anthropogenic effects, cold shock, cold stress, management, physiological stress, thermal stress

## 1 | INTRODUCTION

Temperature plays a manifold role in virtually all biological processes in fish, including physiological stress responses (Madeira *et al.*, 2013), metabolic function (Johnston & Dunn, 1987), immune function (Karvonen *et al.*, 2013; Tort *et al.*, 2003), individual and population-level growth (Jobling, 1997), foraging behaviour (Alanärä *et al.*, 2001), migration (Jonsson & Jonsson, 2009) and community-level interactions (Taniguchi *et al.*, 1998). With the exception of a relatively small number of species that exhibit varying degrees of regional endothermy (Dickson & Graham, 2004), fish are poikilotherms: their body temperatures depend on and fluctuate with their environments, and they must often rely on behavioural thermoregulation for ideal conditions (Golovanov, 2006). A considerable amount of research on the sublethal and lethal impacts of thermal stress in fish has focused on high temperature stress, which to this day remains one of the most widespread problems in conservation and fisheries management in the context of global climate change (Crozier & Hutchings, 2014; Whitney *et al.*, 2016). Although often overlooked in comparison to heat stress, low temperature stress occurs frequently as a result of

  

both natural (*e.g.*, cold snaps, upwelling events; Hsieh *et al.*, 2008; Hsu & Gwo, 2017) and anthropogenic (*e.g.*, industrial effluent; Michie *et al.*, 2020a) causes. Although the effects of low temperature stress on fish have also been the subject of the study for almost a century (*e.g.*, Doudoroff, 1942), acknowledgement that this too is a facet of the climate change impacts on fishes is both limited and quite recent (Szekeres *et al.*, 2016). Climate change could result in increased variability in weather events, meaning that cold snaps and upwelling could be more frequent and or more severe (ELPC, 2019).

There is no shortage of definitions for "stress," though some are described more frequently than others. Brett (1958) defined stress as "a state produced by an environmental or other factor which extends the adaptive responses of an animal beyond the normal range or which disturbs the normal functioning to such an extent that in either case, the chances of survival are significantly reduced." A more succinct definition was provided by Schreck (2000), who describes stress as the "physiological cascade of events that occurs when the organism is attempting to resist death or re-establish homeostatic norms in the face of insult." The generalized stress response in fish and other organisms can be divided into three roughly sequential categories: primary, secondary and tertiary responses (Barton, 2002; Wendelaar Bonga, 1997). The primary stress response consists of the brain/neuroendocrine response with the release of catecholamines (*e.g.*, epinephrine, norepinephrine and dopamine) and corticosteroids (*e.g.*, cortisol) in response to a stressor (Iwama *et al.*, 1999). Secondary stress responses include changes in metabolism, blood chemistry, osmoregulation, immune and cardiac functions at the cellular and molecular levels, and cellular responses (Barton, 2002; Skomal & Mandelman, 2012). Tertiary stress responses comprise whole-organism health and population-level changes, such as survival, growth and developmental changes, whole-body immune function, oxygen consumption and metabolic rate, and foraging and predation behaviours (Barton, 2002; Wendelaar Bonga, 1997). Stress is also often categorized as either acute or chronic, though the distinction between the two and how they impact an organism (*e.g.*, inducing emergency *vs.* coping responses) are not concrete in the context of multiple or simultaneous stressors (Schreck, 2010). Rapid or extreme changes in temperature may elicit a neuroendocrine stress response with associated physiological alterations (*e.g.*, increases in cortisol) in addition to other physiological changes that are not necessarily part of the generalized stress response such as changes in metabolic rate (Tseng *et al.*, 2014) and cellular membrane fluidity (Buhariwalla *et al.*, 2012). The extent to which low temperatures can lead to acute or chronic stress depends on many factors, but the rates and degrees of temperature change with respect to fishes' normal tolerance ranges are particularly important.

Donaldson *et al.* (2008) provided the first review of cold shock in fishes, introducing cold shock as a rapid decrease in body temperature (and the corresponding stress responses) resulting from an acute decrease in environmental temperature, and highlighted natural and anthropogenic causes of cold shock. The ultimate purpose of this review is to provide an update of our current understanding of cold shock and cold stress in fish by synthesizing what has been learned since Donaldson *et al.*'s (2008) work in a comprehensive literature review (see Literature Search Methods section for details). Although a decade is not that long a period, there have been a number of innovations in research methods (*e.g.*, "omics" technologies) and growing interest in the cold side of climate change such that there has been a substantial amount of new work on cold shock and cold stress. Moreover, there is growing recognition that it is important to update reviews periodically (Garner *et al.*, 2016; Shojania *et al.*, 2007) given the strong reliance on evidence syntheses by the scientific community (Donaldson *et al.*, 2011) and decision makers (Cook *et al.*, 2013). We begin by discussing the use of terms such as cold shock and cold stress in the literature, and their distinctions (or lack thereof) as biologically relevant phenomena. As with Donaldson *et al.* (2008), we dedicate much of this review to the generalized stress response in fish as it pertains to cold shock/stress, with focus on how our knowledge has or has not evolved following generally considerable research outputs over the last 12 years. Nonetheless, we try to avoid overlap or redundancy except insofar as is necessary to discuss critical underlying concepts and describe the evolution of the cold shock literature. Readers who have not previously read Donaldson *et al.* (2008) are highly encouraged to do so. Notably, Figure 1 from Donaldson *et al.* (2008) remains an accurate and worthwhile summary of the effects of cold shock on the generalized stress response in fish. We conclude with a discussion of applications of cold shock and recommendations for researchers, management authorities and professionals in relevant sectors (*e.g.*, power generation, fisheries), and highlight high-priority topics for future research.

## 2 | LITERATURE SEARCH METHODS

Literature searches were conducted using two bibliographic databases: (a) Web of Science Core Collections (WoSCC; accessed through Carleton University's institutional subscriptions), and (b) Scopus (Carleton University's institutional subscription) and the Federal Science Library (FSL; a Government of Canada repository of departmental publications, reports and data sets, containing both commercially published and grey literature). Results from each database were restricted by date of publication, beginning with 2008 and including results published up until and including 15 July 2020. Note that because of limitations in the ability to filter by date and export search results using the current FSL search interface, an older FSL interface was used to conduct the search in this database (accessed online *via* http://fsl-bsf.summon.serialssolutions.com/#!/). The search strings were developed and modified through a scoping exercise using WoSCC and Scopus to optimize the use of search terms, wildcards and Boolean operators. The comprehensiveness of the searches was tested against a collection of 10 benchmark articles to ensure articles identified as relevant were being captured in the searches. The specific search strings used for each database, restrictions on search results and results tracking across searching/screening procedures are presented in Table 1. All extracted results from WoSCC, Scopus and the FSL were imported into EndNote Online as individual groups.

**TABLE 1** Search strings used to conduct literature searches, along with details of search restrictions and results for each of the three publication databases

| Search engine | Search string | Restrictions/notes | Results (date) |
|---|---|---|---|
| Web of Science Core Collections | TS = ((“cold shock” OR “cold shock*” OR “cold stress” OR “cold water pollution” OR “cold water thermal pollution” OR “temperature stress” OR “thermal shock$” OR “thermal stress”) AND (*omic$ OR behavio* OR biochemi* OR blood OR geneti* OR h$ematolog* OR “heat shock” OR lethal OR mortalit* OR physiolog* OR stress OR sub$lethal OR surviv*) AND (actinopterygii OR agnatha OR cartilaginous OR chondrichthyes OR elasmobranch OR fish OR fishes OR *fish OR jawless OR “lobe-finned” OR “ray-finned” OR sarcopterygii OR teleost)) | • 2008–present<br>• All languages<br>• All document types | 835 (15 July 2020) |
| Scopus | TITLE-ABS-KEY((“cold acclim*” OR “cold shock” OR “cold shock*” OR “cold stress” OR “cold water pollution” OR “cold water thermal pollution” OR “temperature change” OR “temperature stress” OR “thermal shock$” OR “thermal stress”) AND (*omic OR behavio* OR biochemi* OR blood OR geneti* OR h*ematolog* OR “heat shock” OR lethal OR mortalit* OR physiolog* OR stress OR sub*lethal OR surviv*) AND (actinopterygii OR agnatha OR cartilaginous OR chondrichthyes OR elasmobranch OR fish OR fishes OR *fish OR fish* OR jawless OR “lobe-finned” OR “ray-finned” OR sarcopterygii OR teleost)) AND (LIMIT-TO (PUBYEAR, 2020) OR LIMIT-TO (PUBYEAR, 2019) OR LIMIT-TO (PUBYEAR, 2018) OR LIMIT-TO (PUBYEAR, 2017) OR LIMIT-TO (PUBYEAR, 2016) OR LIMIT-TO (PUBYEAR, 2015) OR LIMIT-TO (PUBYEAR, 2014) OR LIMIT-TO (PUBYEAR, 2013) OR LIMIT-TO (PUBYEAR, 2012) OR LIMIT-TO (PUBYEAR, 2011) OR LIMIT-TO (PUBYEAR, 2010) OR LIMIT-TO (PUBYEAR, 2009) OR LIMIT-TO (PUBYEAR, 2008)) | • 2008–Present<br>• English only<br>• All document types | 1447 (15 July 2020) |
| Federal Science Library | ((TitleCombined:((“cold acclim*” OR “cold shock” OR “cold shock*” OR “cold stress” OR “cold water pollution” OR “cold water thermal pollution” OR “temperature change” OR “temperature stress” OR “thermal shock$” OR “thermal stress”) AND (transcriptomi* OR genomi* OR proteomi* OR metabolomi* OR behavio* OR biochemi* OR blood OR geneti* OR hematolog* OR haematolog* OR “heat shock” OR lethal OR mortalit* OR physiolog* OR stress OR sub*lethal OR surviv*) AND (actinopterygii OR agnatha OR cartilaginous OR chondrichthyes OR elasmobranch OR fish OR fishes OR fish* OR jawless OR “lobe-finned” OR “ray-finned” OR sarcopterygii OR teleost)) OR Abstract:((“cold acclim*” OR “cold shock” OR “cold shock*” OR “cold stress” OR “cold water pollution” OR “cold water thermal pollution” OR “temperature change” OR “temperature stress” OR “thermal shock$” OR “thermal stress”) AND (transcriptomi* OR genomi* OR proteomi* OR metabolomi* OR behavio* OR biochemi* OR blood OR geneti* OR hematolog* OR haematolog* OR “heat shock” OR lethal OR mortalit* OR physiolog* OR stress OR sub*lethal OR surviv*) AND (actinopterygii OR agnatha OR cartilaginous OR chondrichthyes OR elasmobranch OR fish OR fishes OR fish* OR jawless OR “lobe-finned” OR “ray-finned” OR sarcopterygii OR teleost)) OR SubjectTerms:((“cold acclim*” OR “cold shock” OR “cold shock*” OR “cold stress” OR “cold water pollution” OR “cold water thermal pollution” OR “temperature change” OR “temperature stress” OR “thermal shock$” OR “thermal stress”) AND (transcriptomi* OR genomi* OR proteomi* OR metabolomi* OR behavio* OR biochemi* OR blood OR geneti* OR hematolog* OR haematolog* OR “heat shock” OR lethal OR mortalit* OR physiolog* OR stress OR sub*lethal OR surviv*) AND (actinopterygii OR agnatha OR cartilaginous OR chondrichthyes OR elasmobranch OR fish OR fishes OR fish* OR jawless OR “lobe-finned” OR “ray-finned” OR sarcopterygii OR teleost)))) | ***Search conducted using old interface – says “594 results”, but includes duplicates → only 497 unique results exported<br>• 2008 – Present<br>• English only<br>• Any content type<br>• Disciplines restricted to: biology, ecology, sciences, environmental sciences, oceanography, zoology, chemistry, anatomy and physiology, veterinary medicine<br>• All formats<br>• Exclude: newspaper articles, book reviews | 497 (15 July 2020) |

*Note*: Strings were divided into three components: (1) phenomenon (*e.g.* “cold shock”, “cold stress”), (2) quantifiable responses in experiments/studies (*e.g.* “behavio*”, “mortalit*”) and (3) taxonomic terms (*e.g.* teleost, fish and elasmobranch).

Duplicate results were initially filtered using the "Find Duplicates" function, eliminating 1 result from WoSCC, 370 from Scopus and 20 from the FSL. The remaining 2388 results were then added to a single group and screened by CHR for relevance at the title and abstract level. At this stage, further duplicates were identified because of minor variations in author names, or special character variants (*e.g.*, "ø" *vs.* "o"), and manually removed ($n = 493$ further duplicates removed from all databases combined).

The 564 unique articles that passed screening at the title/abstract level were then screened at the full article level by CHR for relevance. Articles that passed full-text screening stage were deemed potentially relevant for inclusion in this review only if the article focused on cold shock and/or cold stress, whereas those focusing only on cold acclimatization or cryopreservation were also initially included. Nonetheless, articles focused on cryopreservation were later excluded upon further consideration because these studies typically focused on preservation of fish gametes and addressed questions that fell outside the scope of this work. Likewise, numerous articles focused on cold acclimatization without implications for cold stress or shock (*e.g.*, no experimental investigation of the effects of relevant temperature decreases) and were also excluded. Therefore, a total of 239 articles were included in this updated review (Appendix S1).

## 3 | SHOCK, STRESS OR ACCLIMATIZATION: EVIDENCE FOR BOUNDARIES?

The terms cold acclimatization, cold stress and cold shock are all frequently used in the literature but are often poorly defined. Cold itself is an abiotic stressor, where the term "stressor" refers to the biotic or abiotic causal agent/factor that elicits a stress response (Schulte, 2014). "Cold shock" is a term frequently used to define exposure to abrupt temperature changes, or sharp decreases in temperature over a short time period. Nonetheless, what exactly is considered a sharp decrease or short time period will vary considerably across taxa, populations and systems. There does not seem to be any evidence suggesting the existence of a well-defined boundary between "cold shock" and "cold stress" responses in fish. Instead, both the rate of cooling and the magnitude of temperature change are of major consequence to the stress response that will be elicited in fish (Donaldson *et al.*, 2008), and can help elucidate the potential distinctions between cold shock/stress and the possible subsequent process of cold acclimatization. In discussing literature throughout this review, the terms cold shock and cold stress are used to refer to diverse temperature stress treatments or events in their original contexts [*i.e.*, source material; authors may often use "cold shock" to refer to relatively rapid temperature changes (*e.g.*, instant drops or multiple degrees per hour) while using "cold stress" to refer to more gradual temperature changes (*e.g.*, 1–2°C per day) or long-term holding at suboptimal temperatures], and do not necessarily describe mutually exclusive phenomena that can be readily differentiated from one another in the generalized stress response.

It could, however, be possible to distinguish between physiological changes in response to initial cold shock or stress *vs.* those associated with acclimatization to low temperature environments. The changes in primary, secondary and tertiary stress responses after initial cold shock or stress can be monitored to see if they change further to states wherein coping and long-term survival may be possible (acclimatization), or if coping is unachievable and the fish is stuck in chronic stress until death or a return to tolerable temperatures (illustrated conceptually in Figure 1). As an example, the tissue-specific transcription of certain genes (*e.g.*, SCD, responsible for the production of stearoyl-CoA 9-desaturase enzymes implicated in fatty acid alteration and maintaining cell membrane fluidity) may be useful in distinguishing between a cold shock/stress response and cold acclimatization, as the initial

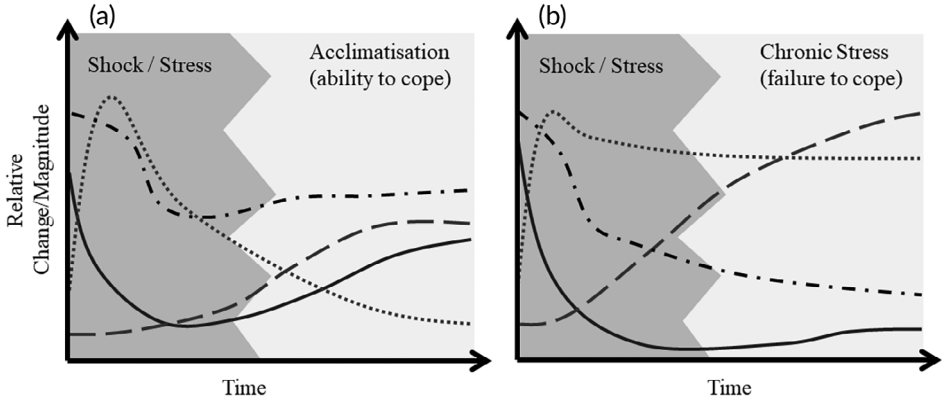


**FIGURE 1** Some hypothetical changes that might be observable in some physiological stress markers (plasma cortisol, dotted line; food intake, solid line; damage from oxidative stress, long-dashed line; disease resistance, dot-dashed line) following initial cold shock or stress in a fish that is either able to acclimatize (a) or fails to acclimatize (b) to low temperatures. This depiction is simplified and does not illustrate complexities such as the rate or degree of temperature change, but illustrates conceptually how stress markers might respond in various detectable ways that may be useful in drawing distinctions between a fish experiencing acute stress, chronic stress or acclimatization

stress response and subsequent coping (if possible) can elicit different, characterizable transcription patterns (*e.g.*, Trueman *et al*., 2000). Nile tilapia (*Oreochromis niloticus* L. 1758) that were acutely cold shocked (23 to 12°C) for 48 h did not exhibit elevated SCD transcription levels in liver, muscle or gill tissues, whereas fish acutely exposed to 14°C water for 7 days exhibited upregulated SCD transcription in muscle and gill tissues relative to control individuals maintained at 28°C (Zerai *et al*., 2010). If similar patterns or trends can be substantiated in other stress markers, we may begin to form meaningful ways of assessing cold stress and acclimation status, depending on the species and the nature of cold exposure itself.

The rate of temperature decrease, the magnitude or severity of cooling and the duration of exposure to cold temperatures can all influence the observable changes in physiology and behaviour that follow. Consider the following examples of experiments that illustrate this complexity in the context of cold shock, stress and/or cold acclimatization. Foss *et al*. (2012) exposed Atlantic salmon (*Salmo salar* L. 1758) to temperature changes from 16°C to either 4 or 0°C over both 5 and 1 h cooling periods, noting significant increases in primary (plasma cortisol) and secondary (whole blood lactate, glucose and $Na^+$) stress markers occurring only in the group exposed to 16 to 0°C over 1 h (these parameters did not differ significantly from the control group in the other treatments). Rossi *et al*. (2017) exposed tamuatá (*Hoplosternum littorale* Hancock 1828) acclimatized to 25°C to both acute (1 day) and chronic (21 days) thermal stress by decreasing water temperatures to 10°C (1°C per day). They reported that relative to the control group, acute cold stress led to elevated blood glucose levels and depressed antioxidant enzyme activity in the kidneys, liver and gills, whereas chronic cold stress led to decreased blood glucose, increased liver protein content and elevated lipid peroxidation in the kidneys, liver and gills. Common to both exposure times were an increase in blood triglyceride levels, a decrease in glycogen reserves and increase in lipid content in the liver (Rossi *et al*., 2017). The acclimatization process may be associated with an improved capacity to meet energy demands through lipid metabolism, even though oxidative stress may have been more severe in the long term (Rossi *et al*., 2017). The routine metabolic rates ($MO_2$), maximum $MO_2$ and aerobic scopes of mummichog (*Fundulus heteroclitus* Linnaeus 1766) were nearly halved when cold shocked (15 to 5°C in 15 min) compared with individuals maintained at 15°C; after being held at 5°C temperatures for 6 weeks, the routine $MO_2$ of the cold-shocked (now cold acclimatized) fish had further decreased by *c*. 40%, while maximum $MO_2$ and aerobic scopes remained unchanged (Healy *et al*., 2017). In practice, cold acclimatization may therefore be best characterized by metabolic and other physiological changes that are indicative of coping (or attempts to cope) with long-term exposure to suboptimal temperatures. As we discuss the current knowledge of cold shock/stress and the generalized stress response in fish, note that the considerable variation across taxa and experimental protocols often makes direct comparisons challenging.

## 4 | COLD STRESS AND THE GENERALIZED STRESS RESPONSE IN FISH

### 4.1 | Primary stress response

#### 4.1.1 | Neurological system responses

Donaldson *et al*. (2008) noted that cold shock, as well as acclimatization temperature, can influence the performance and function of neurons in the brain, but the underlying mechanisms by which the brain compensates for cold shock-induced impairments remain poorly understood. Since 2008, several experiments have shed some light on changes in protein expression and metabolite concentrations in the brains of cold stressed fish. Transcription levels of hypoxia-inducing factor 2α (HIF2α, implicated in cellular hypoxia responses) in the brains of Korean rockfish (*Sebastes schlegelii* Hilgendorf 1880) increased by roughly threefold following acute cold shock (16 to 5°C for 12 h; Song *et al*., 2019b); although not "statistically significant," low sample sizes may have masked statistical demarcation of a biologically relevant effect in this case. Increases in HIF2α and other hypoxia-inducing factors are conceivable because of restricted blood flow following cold stress, which may be an adaptive response to reduce the rate of brain cooling during exposure to low temperatures (Donaldson *et al*., 2008). Transcription rates of metallothionein 1 (MT-1), but not metallothionein 2 (MT-2), increased in common carp (*Cyprinus carpio* L. 1758) olfactory bulbs, midbrains and cerebella (Ali *et al*., 2009). Gene transcription associated with the production of heat shock protein 90 (HSP90, a molecular chaperone) was elevated in the brains of grass carp (*Ctenopharyngodon idella* Valenciennes 1844) following acute cold shock (Wu *et al*., 2012), as was stearoyl-CoA-desaturase 1 (SCD1) transcription in large yellow croaker (*Larimichthys crocea* Richardson 1846; Xu *et al*., 2015) and AMPK transcription (resulting in the production of 5′ AMP-activated protein kinase, which plays a key role in regulating energy metabolism) in olive flounder (*Paralichthys olivaceus* Temminck & Schlegel 1846; Nie *et al*., 2020). Interestingly, HSP60 expression in the brains of great albino northern snakehead (*Channa argus* Cantor 1842) decreased following cold shock (Zhou *et al*., 2018a). Metallothionein synthesis may have been upregulated to protect the brain against oxidative stress at low temperatures (Ruttkay-Nedecky *et al*., 2013), and SCD1 has been implicated in the alteration of fatty acids in cell membranes under low temperatures (Hsieh & Kuo, 2005), helping the brain to maintain membrane fluidity during cold stress. Thus, the overall changes in gene expression in the brain following cold shock/stress appear to reflect a suite of protection against the formation of reactive oxygen species (ROS) in the brain and mitigating cellular damage and membrane disruption, a conclusion further supported by studies of other molecular responses to cold shock in the brain.

Prolonged (4 days) cold stress (20 to 4°C) in Amur sleeper (*Perccottus glenii* Dybowski 1877) resulted in a tendency for brain tissues to accumulate free amino acids and other protein constituents (*e.g.*, phosphoserine) that are rich in phosphorus, likely as a means of maintaining cellular membrane fluidity under suboptimal temperatures

and possibly due in part to low temperature-induced protein degradation (Karanova, 2018). Other organs and tissues may show different responses that must be characterized separately; for instance, the author also observed that the livers had been accumulating more sulphur-rich compounds (*e.g.*, taurine; Karanova, 2018). Given the duration of exposure in Karanova's (2018) experiment, future time course experiments might investigate whether such changes in brain free amino acid/protein constituent pools might not have been induced by the shock itself so much as subsequent acclimatization to the new temperature.

Cold shock can induce oxidative stress in the brain, as in other tissues. Tseng *et al.* (2011) reported changes in biomarkers of oxidative stress in the brains of zebrafish (*Danio rerio* Hamilton 1822) acclimatized to 28°C and cold shocked at 18°C for 1, 6 or 24 h. Protein carbonyl concentrations (produced *via* oxidation of protein side chains by ROS; Dalle-Donne *et al.*, 2003) were elevated at 1 h, decreased to below baseline values by 6 h and were elevated again by 24–72 h post-exposure (Tseng *et al.*, 2011). Furthermore, enzymes involved in the destruction or prevention of ROS [superoxide dismutase (SOD), catalase (CAT) and several uncoupling proteins] showed higher production and/or activity levels in the zebrafish brains (Tseng *et al.*, 2011). Using a similar cold shock protocol, Tseng *et al.* (2014) found increased activity of lactate-mobilizing monocarboxylate transporters, proposing that increased lactate transport into zebrafish brains occurs following cold shock to provide an extra source of energy under low temperature stress. Using cold-shocked (27 to 16°C for 72 h) green chromide cichlids (*Etroplus suratensis* Bloch 1790), Joy *et al.* (2017) reported elevated CAT activity in the brain by 24 h (which decreased but remained above baseline levels over the remaining 72 h) and glutathione peroxidase (GPx) only at 48 h post-exposure, whereas SOD activity remained constant over the first 24 h, decreased by 28 h and then increased above baseline levels by 72 h.

In olive flounder, cold stress (18 to 12°C over 8 days) elevated plasma cortisol concentrations over the first 2 days of exposure, and increased the expression of corticotropin-releasing hormone (CRH) over 2 days and urotensin II (UII) over the first several hours post-exposure in the caudal neurosecretory system (CNSS; Yuan *et al.*, 2020). The CNSS is unique to teleost fish, serving as a production site for stress response-regulating hormones such as CRH (which assists with the regulation of physiological and behavioural stress responses, including neuroendocrine parameters and cortisol) and UII (which assists with osmoregulation) (Bernier *et al.*, 2008; Pearson *et al.*, 1980; Yuan *et al.*, 2020). Overall, however, the role of the CNSS in regulating cold stress responses in fish and how cold stress relate to neurophysiological changes at the brain/CNS level have not been extensively studied.

### 4.1.2 | Endocrine responses

Donaldson *et al.* (2008) described some works demonstrating that catecholamines (*i.e.*, epinephrine, norepinephrine and dopamine) are detectable in blood plasma earlier than cortisol and can be used as potential indicators of acute cold stress in fish. Nonetheless, we have identified no new studies since 2008 that measured the production, concentrations or movements of catecholamines in fish following cold shock or cold stress.

A large number of experiments have quantified whole-body, serum or plasma cortisol concentrations following cold shock/stress, generally reporting increases in cortisol and delayed recovery expected in cold-stressed fish (Donaldson *et al.*, 2008). Generally, cortisol peaks within the first few hours following cold shock (*e.g.*, Koakoski *et al.*, 2012; Trushenski *et al.*, 2012), but may not return to pre-stress levels as long as cold exposure continues. In "genetically improved farmed tilapia" ("GIFT," an *O. niloticus* strain which has undergone extensive selective breeding), acute cold shock from optimal temperature (28 to 13°C) greatly increased serum cortisol concentrations, which remained elevated until sampling ended at 120 h post-shock (He *et al.*, 2015). Mattioli *et al.* (2020) cold shocked juvenile *Lophiosilurus alexandri* Steindachner 1876, a tropical catfish, for 24 h (28 to 18°C) and observed increases in plasma cortisol 1 h post-transfer, and less elevated (but still above baseline) cortisol levels by the end of the 24 h exposure period. A brief cold shock (28 to 18°C for 5 min) increased the ratio of whole-body cortisol/total protein content in larval zebrafish (Bai *et al.*, 2016). Ji *et al.* (2016) rapidly cooled turbot (*Scophthalmus maximus* L. 1758) from 18 to 1°C, which increased plasma cortisol as temperatures fell below *c.* 12°C.

The changes in circulating cortisol concentrations observed following cold shock/stress is dependent on the rate, magnitude and duration of temperature change (Donaldson *et al.*, 2008). Korean rockfish that were either cold shocked (abrupt transfer from 20 to 14°C and back to 20°C after 24 h) or more gradually cold stressed (20 to 14°C at 2°C per day, then returned to 20°C) and exposed to light stress treatments exhibited elevated plasma cortisol (and glucose) levels at the lower temperature, but the increase in plasma cortisol elicited by the abrupt cold shock was greater than the gradually stressed group (Choi *et al.*, 2017). Choi *et al.* (2017) also reported the same trend in plasma glucose, a secondary stress biomarker that can be loosely correlated with cortisol as the latter promotes glycogenolysis and the mobilization of glucose in the blood (Mommsen *et al.*, 1999). Largemouth bass (*Micropterus salmoides* Lacepède 1802) acclimated to 20°C water exhibited an increase in plasma cortisol after 1 h exposure to 8°C, but not at 6 h post-exposure to 18°C or at 1 or 6 h post-exposure to 15°C, with the same general trend visible in the plasma glucose profiles as well (VanLandeghem *et al.*, 2010).

Nonetheless, some experiments (all on tropical/subtropical freshwater teleosts) have failed to observe cold-induced cortisol increases. Adloo *et al.* (2015) observed similar gradual increases in serum cortisol over 24 h in both an ambient control group and a cold shock (*c.* 27.5 to 15°C for up to 24 h) group of iridescent shark catfish (*Pangasianodon hypophthalmus* Sauvage 1878). Likewise, the transient increases in plasma cortisol over 24 h did not differ between cold-shocked (28 to 18°C for 1 h) matrinxã (*Brycon amazonicus* Agassiz 1829) relative to a handling control (Inoue *et al.*, 2008). Plasma cortisol did not differ between cold-shocked bonefish (*Albula vulpes* L. 1758)

exposed to two different temperature changes ($\Delta T = -7$ and $-14^{\circ}C$) for 2 h, or a handling control (Szekeres *et al*., 2014). Further investigation of the initial brain responses to cold stress [recommended by Donaldson *et al*. (2008) but having received little attention since] could help explain why clear differences in cortisol, a normally reliable indicator of stress, may not be observed in response to cold stress unless the lack of detectable differences in cortisol levels is the result of confounding stress that may originate from handling and/or holding conditions (*e.g*., Portz *et al*., 2006; Pottinger *et al*., 1992).

## 4.2 | Secondary stress response

### 4.2.1 | Haematological parameters

The changes in blood metabolite and other haematological responses following cold stress are highly variable across species, life-history stages, diurnal variations and other environmental parameters such as water chemistry (Donaldson *et al*., 2008). Haematological responses are also susceptible to further change from additional interacting stressors. Nonetheless, cold stress may prolong both the time required for many secondary stress biomarkers to demarcate physiological stress and also the time necessary for the same biomarkers to recover to pre-exposure levels (Donaldson *et al*., 2008). Such delays could partially explain the inconsistencies in common secondary stress biomarkers (*e.g*., blood glucose) reported following cold stress.

Overall, blood glucose concentrations appear to change in response to energetic demands associated with varying degrees of cold exposure, with initial increases typical of a stress response followed by decreases in the long term as fish transition towards lipid metabolism and other viable energy sources. Whole-blood glucose concentrations in checkered puffers (*Sphoeroides testudineus* L. 1758) were elevated following an acute cold shock (*c*. 29 to 24°C for 4 h) relative to fish exposed to heat shock or an ambient control (Cull *et al*., 2015). Serum glucose in GIFT tilapia increased following acute cold shock, returning to baseline levels by 72 h post-shock and decreasing below baseline levels by 120 h post-shock (He *et al*., 2015). The authors also reported a transient increase in serum triglycerides (returning to baseline levels by 72 h post-shock) and a chronic decrease in serum cholesterol (which lasted until the end of sampling at 120 h post-shock), and a number of other impacts on lipid metabolism that indicate a high energetic demand from prolonged cold stress (He *et al*., 2015). A similar trend in serum glucose over a longer cold stress period (28 to 15°C, 1°C per h for up to 5 days) was seen in GIFT tilapia in another experiment (Shi *et al*., 2015). Panase *et al*. (2018) cold stressed Nile tilapia (25 to 13°C at 3°C per h, held at 13°C for up to 3 days) and observed initial decreases followed by gradual increases in serum glucose and nitrogenous waste in the blood over the sampling period, along with fluctuations in serum cholesterol and gradual increases in alanine and aspartic transaminases likely released into the bloodstream as a result of liver damage. Nonetheless, relative to ambient temperature controls, serum glucose levels did not change following 24 h cold shock (*c*. 27.5 to 15°C) in iridescent shark catfish, though both control and cold-shocked groups exhibited slight fluctuations over the 24 h period (Adloo *et al*., 2015). Blood glucose in bonefish was unaffected by 2 h exposure to a decrease in temperature by 7 or 14°C; nonetheless, blood lactate was elevated in the −14°C group relative to a handling control (Szekeres *et al*., 2014). In small-scale pacu (*Piaractus mesopotamicus* Holmberg 1887) exposed to cold stress (either 24 to 21 or 18°C, at 0.6 or 1.2°C per h, respectively), blood glucose decreased and blood lactate and pH increased, relative to a control group (Pinto *et al*., 2019). Milkfish (*Chanos chanos* Fabricius 1775) exposed to low temperature stress (28 to 18°C for 7 days) exhibited decreased blood glucose concentrations and no changes in plasma lactate when kept in fresh water, whereas individuals in sea water exhibited elevated blood glucose concentrations and decreases in plasma lactate relative to fish kept at 28°C (Chang *et al*., 2020). In addition, the authors reported increased anaerobic respiration in white and red muscle tissues regardless of salinity (Chang *et al*., 2020). Changes in blood glucose may therefore be part of the adaptive, beneficial value of an acute stress response (eustress), and it is possible that a lack of detectable responses might be indicative of a fish's inability to respond to cold shock or stress. Conversely, rapid decreases in blood glucose, with little or no initial increases, could suggest an adaptive capacity to rapidly switch towards other energy sources such as lipid metabolism (Wen *et al*., 2018). Elevations in lactate occur frequently after exercise and movement resulting in anaerobic swimming (Hammer, 1995). For fish that show reduced swimming activity following cold exposure, one plausible explanation for observed blood lactate increases is cold-induced increases in adenosine (Eckerle *et al*., 2008), which in turn has vasoconstrictive effects (Soldatov, 2006) that could result in reduced oxygen supply and therefore elevated anaerobic glycolysis.

Red blood cell abundances, haematocrit (packed red blood cell volume) or haemoglobin concentrations may be measured as indicators of oxygen-carrying capacity in blood (Wells & Baldwin, 1990). Changes in white blood cell abundances are elicited by disease, infection, inflammation and other immunological burdens, but may also follow as the immune system is actuated or suppressed by acute or chronic stress, respectively (Clauss *et al*., 2008; Tort, 2011). Cold shock (24 to 14°C) for 24 h did not affect red or white blood cell counts, haematocrit or haemoglobin levels in small-scaled pacu (Bacchetta *et al*., 2020). Haematocrit and haemoglobin levels were likewise unaffected by 1 h cold shock in matrinxã (Inoue *et al*., 2008). Conversely, in juvenile *L. alexandri*, 24 h cold shock induced temporarily (<24 h) depressed white blood cell counts but did not affect red blood cell counts (Mattioli *et al*., 2020). Red and white blood cell counts (or their relative volumes, *i.e*., haematocrit and leucocrit, respectively) are not generally considered reliable indicators of cold stress because they can vary considerably in sensitivity and response even between individuals of the same species, though cold stress can reduce total white blood cell counts or alter levels of specific white blood cell types (Donaldson *et al*., 2008), suggesting possible immunological impairment. Nonetheless, blood cell counts or volumes may still be of value when related to other changes in haematology or immune

function. Orange-spotted grouper (*Epinephelus coioides* Hamilton 1822) acclimatized to 27°C exhibited decreased white blood cell counts 3 h post-transfer to 19°C, which recovered to near control levels at 6 h, then subsequently decreased further over 90 h (Cheng *et al*., 2009). In the same experiment, respiratory burst (ROS release) and phagocytic activity exhibited similar trends, whereas alternative complement pathway (ACP; an innate component of the immune system's protective complement system) and lysozyme activity remained depressed over the 96 h period (Cheng *et al*., 2009). ACP activity was elevated in Mozambique tilapia (*Oreochromis mossambicus* Peters 1852) over 4–24 h following cold stress (*c*. 24–28 to 12°C for up to 48 h), whereas lysozyme activity was also slightly elevated at 4 and 8 h post-exposure (Velmurugan *et al*., 2019).

In turbot maintained at 18°C, Ji *et al*. (2016) reported that rapid cooling (<4°C per h) resulted in sharp decreases in red and white blood cell counts after specific thresholds (*c*. 8 and 5°C, respectively), and plasma glucose concentrations increased with cooling until 1°C where they returned to baseline levels. The authors also observed variable changes in the concentration of enzymes linked to cellular damage in the blood plasma, with alanine transaminase and creatine kinase activity increasing as temperature decreased and remaining elevated at 1°C (Ji *et al*., 2016). Total blood cell counts decreased with cooling (25 to 13°C at 1°C per h) in obscure puffers (*Takifugu obscurus* Abe 1949) relative to an ambient control (Cheng *et al*., 2017); nonetheless, it is unclear whether this decrease in blood cell counts is attributable to changes in red and/or white blood cell levels. Cheng *et al*. (2017) also reported elevated DNA damage in blood cells as temperatures dropped below 21°C, and a transient increase in blood glucose and oxidative stress markers with decreasing temperature, implying reduced viability of all blood cells because of oxidative stress and DNA damage. Which types of blood cells are impacted by cold, and in what manner, has important implications for the nature of physiological impairments imposed by low temperature stress.

### 4.2.2 | Metabolism, oxidative stress and cardiac function

Oxidative stress can be defined as an imbalance between the presence of ROS and antioxidant capacity (*i.e*., the ability to neutralize ROS) in the former's favour, leading to oxidative damage (Biller & Takahashi, 2018; Birnie-Gauvin *et al*., 2017). Cold shock and stress are commonly associated with oxidative stress (*e.g*., increased lipid peroxidation), promoting tissue-specific increases in antioxidant enzyme activity and altered metabolic processes. Oxidative stress can be measured in a number of ways, including indicators of oxidative damage (*e.g*., protein carbonyls, lipid peroxidation and DNA damage) and indicators of antioxidant activity [*e.g*., activity of antioxidant enzymes such as SOD, CAT, glutathione (GSH) or GPx; reviewed in Birnie-Gauvin *et al*., 2017]. Cold-shocked (23 to 17.1°C) Brazilian flounders (*Paralichthys orbignyanus* Valenciennes 1839) exhibited time- and tissue-dependent changes in antioxidant enzyme activity and lipid peroxidation, with cold stress generally inducing short-term (<24 h) increases in lipid peroxidation in the gills and glutathione S-transferase (GST) activity in the liver, and long-term (24–72 h) increases in lipid peroxidation in the liver, decreases in liver and gill CAT activity, and decreases in gill GST activity (Garcia *et al*., 2015). Gilthead seabream (*Sparus aurata* L. 1758) cold stressed for 7 days at 8°C following temperature decrease from 20°C over 3 d displayed increased evidence of oxidative stress and elevated lipid peroxidation in the liver (Ibarz *et al*., 2010). Similarly, Pinto *et al*. (2019) cold stressed small-scale pacu (24 to 21 or 18°C, 0.6 or 1.2°C per h, respectively) and measured reduced overall antioxidant capacity and increased lipid peroxidation rates in the liver. Liu *et al*. (2018a) reported that in both Atlantic salmon and steelhead trout (*Oncorhynchus mykiss* Walbaum 1792) livers, fatty acid compositions changed in response to cold stress (16 to 1°C, 0.5°C per h) through relative increases in the abundances of unsaturated fatty acids, which promote membrane fluidity under cold temperatures at the expense of a reduced capacity to mitigate oxidative stress. Similar changes in phospholipid membrane fatty acid composition were elicited in the brains, spleens, hearts and muscles of steelhead trout under a similar cooling regime (Liu *et al*., 2019a). Joy *et al*. (2017) cold stressed green chromide cichlids for 72 h (27 to 16°C) and found evidence of oxidative stress (*e.g*., elevated SOD, CAT and GPx activity) primarily in the gills and muscles and also in the liver and brain by 48 h of exposure. Zebrafish cold shocked for up to 24 h (28 to 12°C) exhibited signs of oxidative stress and elevated antioxidant enzyme activity (CAT, GPx) and apoptosis rates in the gills and liver compared to an ambient control group (Wu *et al*., 2015). Cinnamon clownfish (*Amphiprion melanopus* Bleeker 1852) acclimatized to 28°C and cold stressed *via* gradual temperature reduction to 20°C (1°C per day) exhibited higher levels of $H_2O_2$ and malondialdehyde (MDA; both indicators of oxidative stress) as well as slight increases in the expression of antioxidant enzymes (CAT, GPx and SOD; Park *et al*., 2011). In GIFT tilapia head kidney tissues, lysozyme and SOD activity decreased, and MDA concentrations increased, over 96 h of cold shock (28 to 9.4°C) relative to an ambient control (Qiang *et al*., 2018). Zutshi *et al*. (2020) describe depressed rates of lipid peroxidation (MDA production) in the gills and muscles of cold-shocked (25 to 15°C for 3 and 6 h) koi (*Cyprinus rubrofuscus* "koi" Lacepède 1803), as well as elevated glutathione (GSH) in the gills and muscles at 3 and 6 h into cold shock. Barramundi (*Lates calcarifer* Bloch 1790) larvae acclimatized to 28°C and cold stressed at 26, 24, 22 or 20°C exhibited elevated SOD activity at 24 or 22°C but not at 20°C, and an inverse relationship between GSH-Px activity and temperature was observed over 72 h; activity trends of other enzymes (*e.g*., POD) were less consistent between time points and temperatures (Tang *et al*., 2018). Thus, there appear to be two general trends in cold-induced oxidative stress: first, oxidative stress tends to increase in most if not all cases of cold shock or stress, and second, antioxidant defences may be initially elevated if temperature decreases are not too drastic, but with sufficiently great and/or rapid temperature drops and lengthening cold exposure, antioxidant defences are likely to be impaired while oxidative damage rate remains high.

Some work has been done on changes in both cellular and organismal metabolism and metabolic flux in response to low temperature stress. After being fasted for 48 h and exposed together to an acute temperature decrease (27 to 20°C), mosquitofish (*Gambusia affinis* Baird & Girard 1853) displayed an innate plasticity in ureotelic *vs*. ammoniotelic nitrogen excretion depending on environmental salinities that was not observed in zebrafish (Uliano *et al*., 2010). Specifically, in mosquitofish, cold shock increased urea excretion rates at low salinity (0‰), decreased urea excretion rates at high salinity (35‰) and generally lowered ammonia secretion rate across a 0–35‰ range of salinities; conversely, zebrafish only exhibited significant decreases in urea and ammonia excretion rates at 25‰ and 10‰ salinities, respectively (Uliano *et al*., 2010). A rapid temperature decrease (28 to 4°C at 4°C per h) was associated with increased accumulation of subdermal lipids 3 days later in pond loach (*Misgurnus anguillicaudatus* Cantor 1842) which were metabolized within a further 7 days (possibly to meet elevated energy demands associated with low temperature stress, likely as part of the acclimatization process; Chen *et al*., 2018).

Oxidative phosphorylation machinery in three *Fundulus* spp. populations was differentially affected by acclimatization temperature (12 and 28°C); following acute temperature change (to 12, 20 or 28°C) or no change, mitochondrial respiration and oxidative phosphorylation enzyme complex activities in the heart typically remained near acclimatization temperature levels at 20°C regardless of whether fish were acclimatized to high or low temperatures, but were typically reduced following more extreme acute temperature changes (*i.e*., 12 to 28°C or 28 to 12°C), suggesting that acclimatization temperature can influence fishes' capacity to maintain cellular respiration in the face of rapid temperature change (Baris *et al*., 2016).

As temperature has often been considered the "master" variable in regulating the rate of physiological processes in fish (Brett, 1971; Gale *et al*., 2013), reversible changes in cardiac function with changing temperature may be apparent under cold shock or stress regardless of the severity (or lack thereof) of the generalized stress response as measured by other metrics. Cooling of isolated zebrafish hearts from 28 to 18°C by 1°C steps (held at each temperature for 2 min) resulted in a *c*. 40% decrease in mean heart rate, prolonged atrioventricular delays by *c*. 7% for every 1°C decrease and increased the duration of action potentials within atria and ventricles; nonetheless, these changes subsided at similar rates when temperature was returned to 28°C at the same rate (Lin *et al*., 2014). The heart rate and velar movement rate (indicative of respiratory activity) both decreased with acute cooling (13 to 7°C over 1.5 h) in New Zealand hagfish (*Eptatretus cirrhatus* Forster 1801; Coxon & Davison, 2011). Heart rate and cardiac output, but not stroke volume, decreased slightly with cooling (5 to 0°C over 5 h) in cunner (*Tautogolabrus adspersus* Walbaum 1792) coupled with a reduction in metabolic rate, all of which were similar but less dramatic than the natural decreases in these responses because of fall/winter cooling (Costa *et al*., 2013). Similarly, heart rate and cardiac output (but not stroke volume) decreased with cooling (12 to 5°C, 1°C per 80 min) in rainbow trout (*O. mykiss*; Petersen *et al*., 2011). The cardiac performance (heart rate, cardiac output and cardiac power output) of shorthorn sculpins (*Myoxocephalus scorpius* L. 1758) was unaffected by an acute temperature decrease (6 to 1°C), temperatures falling within the natural range experienced by these fish (Farrell *et al*., 2013). Atlantic cod (*Gadus morhua* L. 1758) acclimatized to 10°C and cooled to 4°C over 60 min did not exhibit changes in maximum heart rate, cardiac output or stroke volume with cooling, whereas individuals acclimatized to 4°C and cooled to 0°C did exhibit a slight decrease in maximum heart rate (Lurman *et al*., 2012). The ability for fish to maintain adequate cardiac performance in thermally dynamic environments could be a significant factor in a species' ability to maintain pre-existing ranges and colonize new areas (Farrell *et al*., 2013), as well as cope with thermal challenges (*e.g*., cold shock) which occur naturally and may become more frequent as a result of anthropogenically accelerated climate change (Szekeres *et al*., 2016). Mechanisms for cold tolerance in fish hearts have been given some attention, although this also tends to be highly context-specific. In ventricular myocytes of Bluefin tuna (*Thunnus orientalis* Temminck & Schlegel 1844), which experience significant temperature changes during routine swimming and hunting, Shiels *et al*. (2015) demonstrated that cold shock-induced reductions in $Ca^{2+}$ flux and reduced contractility may be mitigatable by elevated adrenaline levels that prolong action potential delays and allow more time for $Ca^{2+}$ movement across L-type $Ca^{2+}$ channels. Further work on isolated European eel (*Anguilla anguilla* L. 1758) hearts has demonstrated that acute low temperature shock can alter the physiological mechanisms underlying the Frank–Starling law (*i.e*., elevated tension on the heart muscles from increased blood inflow results in stronger contractions of said muscles) by decreasing its dependence on nitric oxide modulation, allowing adequate cardiac function to continue following acute temperature change (Amelio *et al*., 2013).

### 4.2.3 | Gene expression, protein activity and other immune parameters

Many changes in gene expression and protein activity have been implicated in cold shock/stress responses in fish, most notably concerning heat shock proteins (HSPs), lactate dehydrogenase (LDH) and other proteins involved in responses to thermal stress, metabolic function and cell/tissue damage. Donaldson *et al*. (2008) described the potential relevance of HSPs and other proteins in the cold shock/stress response and subsequent acclimatization, also noting that (at the time) "omics" approaches to measuring cold stress were still quite recent and that future work was necessary to evaluate the reliability of HSP responses as metrics of cold shock. As with many elements of the generalized stress response described thus far, the magnitude, rate and duration of cold shock/stress are critical, as well as tissue-specific differences in gene expression and protein activity and the potential roles of interacting stressors and intra- and interspecific variation. The formation of HSPs occurs in response to many internal (biological) and external (environmental) stressors, where HSPs serve as molecular chaperones involved in the folding, repair and breakdown of proteins damaged by stressors (Basu *et al*., 2002;

Iwama *et al*., 1998). LDH production is reflective of anaerobic glycolysis rates required to meet energy demands under hypoxia stress (Kyprianou *et al*., 2010). ATPase activity in muscle tissues has previously been shown to increase under cold acclimation (Hwang *et al*., 1990). Together, the synthesis of proteins that assist fish in meeting the physiological demands and mitigating the tissue/cellular damage that follow cold shock is an adaptive response, in the absence of which a fish would likely be less and less able to cope with increasing duration and/or severity of low temperature exposure. For example, LDH activity increased sharply in cold-shocked largemouth bass (20 to 8°C) from 1 h to 6 h during exposure, whereas bass that underwent a lesser temperature decrease (20 to 15°C) did not exhibit changes in LDH activity at 1 or 6 h (VanLandeghem *et al*., 2010). The activities of LDH, myosin ATPase and HSP70 were all elevated within 24 to 48 h of cold shock (20 to 5°C for 72 h) in *Barilius bendelisis* Hamilton 1807 (Kapila *et al*., 2009). HSP70 transcription increased, and gill $N^+/K^+$-ATPase (NKA) transcription and abundance decreased, in response to both cold shock and cold stress in Korean rockfish, with cold shock eliciting greater observed differences in all cases and likely damaging gill tissues (Choi *et al*., 2017). Similarly, immunoglobulin and lysozyme levels in the Korean rockfish plasma were both depressed in cold-shocked and, to a slightly lesser extent, cold-stressed individuals in the same experiment (Choi *et al*., 2017). Basu *et al*. (2015) measured changes in the transcription of genes in major carp (*Labeo catla* Hamilton 1822) implicated in immune function (toll-like receptors and nucleotide-binding oligomerization domain receptors) following cold stress (25 to 20, 15 or 10°C at 2°C per day), finding stress-induced differences in expression patterns between 12 h and 7 days post-exposure to each final temperature (minus 10°C, where 100% mortality was observed at 7 days) indicative of the triggering of innate immune defences against cell damage.

Stress-induced HSP production has been shown to vary across tissues, a phenomenon that (at least in the context of heat stress) has been proposed to be linked to the extent to which specific organs and tissues dictate individual fish's thermal tolerance ranges (Dyer *et al*., 1991), as well as vary with the thermal histories of different species (Dietz & Somero, 1993). Many experiments have investigated cold-induced effects on HSPs using a wide array of species and experimental protocols. Despite the lack of direct comparability between many of these works, overall, it appears that certain organs and tissues (*e.g*., brain, kidney and liver) may have greater capacities to resist degradation and produce damage-mitigating proteins than others (*e.g*., gills). Nonetheless, further research is required on the mechanisms underlying tissue- and life-history stage-specific transcriptional changes in different HSPs in response to cold shock and cold stress. Major carp acclimatized to 28°C and exposed to 25, 20, 15 or 10°C (at 2°C per day decreases) displayed inconsistent but typically upregulated HSP60, HSP70 and HSP90 transcription in muscles, liver and pancreas with cooling (Sharma *et al*., 2017).

HSP70 and HSP90 transcription was elevated in turbot during acute cooling from 18 to 1°C but varied across different tissues and temperatures (Ji *et al*., 2016), with HSP90 being generally more sensitive to temperature changes and brains, head kidneys and kidneys exhibiting relatively high HSP70 expression (and therefore resistance to cold-induced tissue damage) compared to other muscles, gills and other tissues. HSP70, HSP90 and metallothionein (MT-1 and MT-2) transcription in heart tissues variably changed over time following cold shock (12 to 5°C) in common carp, with all gene transcription levels increasing to some degree except MT-1 which decreased over 1–2 h of exposure (Ali *et al*., 2010). HSP70 transcription was significantly upregulated in the kidneys, muscles and fins of striped snakehead (*Channa striata* Bloch 1793) cold shocked (28 to 16°C) for 1 h relative to transcription levels in the liver (which were treated as a baseline) and stomach and gill tissues (which were slightly upregulated; Eid *et al*., 2016). HSP90 transcription was upregulated in the liver, spleen, brain and intestine, but not kidney, in cold-shocked grass carp (4°C for 2 h from an unspecified starting temperature; Wu *et al*., 2012). Common carp cold shocked for 1 or 5 h (12 to 5°C) likewise exhibited tissue-specific changes in heat shock gene transcription: *hsp90a* transcription increased in the skin at both time points, and in the spleen and blood at 5 h; *hsc70-1* transcription increased in the blood at 1 h and in the skin at 5 h; and, *hsc70-2* transcription was depressed in the spleen at 1 h and in the blood at 5 h (Ferencz *et al*., 2012). Interestingly, *hsp70* transcription was only slightly elevated in the blood at 1 h relative to baseline levels (Ferencz *et al*., 2012). Cold-stressed major carp (28 to 15°C, 1°C per h for up to 5 days) had elevated HSP70 transcription in both muscle and liver tissues within 12 h of cold exposure (during which time SOD and CAT enzyme activities also peaked), which gradually decreased to slightly above baseline levels by 5 days (Shi *et al*., 2015). HSP70 expression in cold-shocked rohu (*Labeo rohita* Hamilton 1822; 26 to 4°C for 3 h) was most elevated in the spleen and liver, and also in the kidney and muscle with respect to a control group (Giri *et al*., 2014). In another freshwater tropical species, juvenile streaked prochilod (*Prochilodus lineatus* Valenciennes 1837), HSP70 abundance was initially depressed following transfer from 25 to 20°C water for 1 h, but by 4 h HSP70 abundance was elevated above baseline levels (Sales *et al*., 2019). Relative to an ambient control (16°C), kaluga sturgeon (*Huso dauricus* Georgi 1775) cold shocked at 4 or 10°C for 2 h displayed elevated transcription levels of HSP70 in muscle and liver tissues at 4°C and in the gills at both temperatures, whereas HSP90 transcription was elevated in the liver at 4°C and in the muscle and gills at both temperatures (Peng *et al*., 2016). Although most research has focused on HSP70 and/or HSP90, other proteins in the HSP family have been investigated as well. Small HSP27 has been implicated in the low- and high-temperature stress responses of large yellow croakers, being primarily expressed in the heart and upregulated in response to cold shock (27 to 19°C) over a 48 h period (Yang *et al*., 2012). Cold-shocked great albino northern snakehead (26 to 8.5°C for 2 h) did not exhibit thermal stress-induced changes in HSP90 expression in the kidney, muscle, spleen or liver (Zhou *et al*., 2017), but did result in significant down-regulation of HSP60 in the brain (Zhou *et al*., 2018a). Both white sturgeon (*Acipenser transmontanus* Richardson 1836) and green sturgeon (*Acipenser medirostris* Ayres 1854) exhibited similar location-specific levels of HSP70 activity following cold shock (18 to 10°C for

2 h) except for in the mucus which, despite being the site of the highest activity for both species, was higher in white sturgeon (Wang *et al*., 2013).

The synthesis and activities of other proteins following cold shock and stress have also received a fair amount of study since 2008, typically concerning genes involved in the production of proteins involved in metabolism, molecular chaperoning or ROS management. Like the oxidative stress responses discussed in the previous section, changes in transcription patterns may reflect a capacity or inability to cope depending on the severity of cold shock/stress. As with HSPs, variations in species, thermal histories and tissues may lead to differential responses to low temperature stress. Cold shock in common carp (12 to 5°C for 1 or 5 h) suppressed *gpx4b* (a gene implicated in GPx production) transcription in the olfactory lobe at both time points, elevated *gpx4b* transcription in the liver after 1 h but depressed transcription by 5 h post-exposure, and depressed *gpx4a* (another gene involved in GPx production) transcription in the liver only at both time points (Hermesz & Ferencz, 2009). Milkfish acclimatized to either fresh water or sea water exhibited elevated transcription levels of the *Ccprdx6* gene (encoding for production of the antioxidant Prdx6) in the liver following cold stress (28 to 18°C, decreasing 2°C per h), though more rapid increases in transcription rates but lower overall antioxidant levels in the freshwater group imply these individuals were more susceptible to oxidative stress than the seawater group (Chang *et al*., 2016a). In olive flounders, dramatic differences were observed in tissue-specific expression of genes coding for AMPK (5′ AMP-activated protein kinase), an enzyme involved in maintaining homeostasis by promoting ATP synthesis; all such genes were upregulated to various degrees in the brain over 28 h of cold shock at 0.2°C following acclimatization at 11°C, but other tissues such as muscles showed less consistent trends (Nie *et al*., 2020). Juvenile barramundi cold shocked for up to 24 h at 16°C (unspecific starting temperature) exhibited sharp decreases in calreticulin (CRT, a molecular chaperone) transcription by 30 min, increasing gradually but still well below baseline levels over 24 h (Bai *et al*., 2012). Cold stress induced downregulation of *scd1* (producing stearoyl-CoA-desaturase 1) transcription in the livers of cold-stressed (15 to 7°C at 2°C per day) large yellow croaker during the first half of cooling, upregulated at temperatures approached 7°C, and downregulated again upon temperature stabilization (Xu *et al*., 2015). Chen *et al*. (2019a) determined that *tmbim3a/grinaa* transcription is important in promoting survival and resilience to cold stress in zebrafish larvae (28 to 16°C for 10 days) by decreasing the risk of cold-induced apoptosis. Qi *et al*. (2011) identified a C3 protein in orange-spotted grouper, the expression of which is elevated following cold shock (25 to 15°C for 36 h) and may be linked to antioxidant defence. In similar experiments with the same general cold shock regime, Qi *et al*. identified elevated respiratory burst activity over 36 h post-shock (2012), as well as elevated p53 protein expression and increased apoptotic total blood cell counts (2013). The upregulation of p53 and genes implicated in mitigating thermal and oxidative stress and cellular damage (*e.g*., CAT, HSP90, C3) was also observed in obscure puffers following cold stress (25 to 13°C, 1°C per h; Cheng *et al*., 2017).

There is also a diverse collection of proteins known as cold shock proteins (CSPs) which are implicated in prokaryotic responses to cold shock, and though less well understood are also present in eukaryotes and may play roles in regulating cell growth and development under cold stress and other conditions (Mihailovich *et al*., 2010; Phadtare *et al*., 1999). The transcription of one such protein, Y-Box-binding protein 1 (YB-1), increased in the spleens and livers of mandarin fish (*Siniperca chuatsi* Basilewsky 1855) between 2 and 12 h post-cooling from 27 to 15°C, but did not significantly change in the liver (He *et al*., 2019). He *et al*. (2019) also reported transient increases in the transcription of *Hsc70a* in the liver and spleen, *p53* in the liver and kidney and decreases in *Hsc70b* in the liver, spleen and kidney over the same time period. Although higher than an ambient control, neither *yb-1* nor *hsp70* transcription differed between cold-tolerant and cold-sensitive olive flounders following cold stress (15 to 0.7°C, *c*. 1°C per h), however, strain-dependent differences in single-nucleotide polymorphisms (SNPs) for *hsp70* genes were observed, and cold-tolerant individuals had higher pyruvate kinase activity and ATP reserves than cold-sensitive fish (Nie *et al*., 2019a). Cold-induced RNA-binding protein (*cirbp*) and high-mobility group box 1 (*hmgb1*) gene transcription were both upregulated in the gills of zebrafish cooled from 28 to 12°C (3°C per h) after 1 day, with *cirbp* transcription returning to baseline levels whereas *hmgb1* remained upregulated after 3 days at 12°C (Chou *et al*., 2008).

Changes in amino acid pools, which tend to vary in relative composition and abundances between organs and tissues and are critical in the synthesis of new proteins and other essential functions under stressful conditions (Jürss & Bastrop, 1995), are generally poorly studied in the context of cold shock/stress in fish. Free amino acid pools in Amur sleeper blood, muscles and brains exhibited major changes in relative amino acid abundances over 4 days of cold shock (8 to 0°C, 1.5°C per h; Karanova, 2011). Notably, the concentrations of most amino acids in muscle tissues had decreased after 2 days (possibly having been appropriated for the synthesis of new proteins involved in the cold stress response) and then increased above baseline levels in most cases after 4 days, whereas brain amino acid abundances generally decreased over 2–4 days (Karanova, 2011). Thus, further study is needed on changes in free amino acid concentrations in organs and tissues such as taurine (*e.g*., Karanova, 2013), which is implicated in immune, antioxidative and signalling functions, among others (Salze & Davis, 2015).

Within species, or populations, individuals may exhibit cold-sensitive or cold-tolerant traits that appear to have a substantial genetic basis. Olive flounders acclimatized to 11°C sea water and cold stressed down to 0.2°C (*c*. 1°C decrease per h) for up to 14 h displayed either tolerance or intolerance to the stress (based on ability or inability to maintain swimming behaviour), with cold-tolerant individuals exhibiting elevated mRNA expression for aerobic metabolism-related proteins (*e.g*., LDH; Lu *et al*., 2018). Similarly, Liu *et al*. (2020) characterized differential transcription patterns in cold-sensitive and cold-tolerant redlip croaker (*Larimichthys polyactis* Bleeker 1877), where cold-tolerant individuals were distinguished from cold-sensitive ones by the former's ability to retain swimming abilities following

rapid cooling (14 to 4°C at 2°C per h, held at 4°C for 3 h). There is also some evidence suggesting that cold-adapted fish can have noticeably different gut microbiomes than cold-sensitive conspecifics (Kokou *et al*., 2018), which warrants further exploration.

Indeed, much work has been done in certain species on characterizing both the number of genes that code for individual proteins implicated in cold shock/stress (*e.g*., HSP70) and large-scale changes in gene expression patterns following low temperature stress compared to non-stressed conspecifics. Because of the sheer volume of data generated, we are unable to adequately summarize all relevant findings from such experiments here. Thus, they primarily provide some contextual information for each experiment and instead direct interested readers to the original research articles. Borchel *et al*. (2017) identified genes that exhibited generally mild up- or downregulation changes in response to cold stress in two rainbow trout strains but noted that many changes were not conserved across both strains. Nitzan *et al*. (2019) described differences in the transcription patterns of blue tilapia (*Oreochromis aureus* Steindachner 1864) that were considered either resistant or sensitive to cold stress based on the survival of closely related fish under prolonger cold stress. Xu *et al*. (2018b) identified 17 different HSP70 genes in large yellow croaker, with differential expression patterns overall in liver tissues in response to cold stress. Transcriptomic characterization of the cold stress (22 to 9°C over 12 h) response in the livers of large yellow croaker was also undertaken by Qian and Xue (2016), with many of the major identified changes in gene expression concerning various metabolic processes (*e.g*., glycolysis, gluconeogenesis; steroid and carbohydrate metabolism, oxidative stress). Sun *et al*. (2019b) described orange-spotted grouper liver transcriptomes following cold stress (28 to 13°C, 1°C per h), and under the same protocol Sun *et al*. (2019a) describe corresponding incidences of blood cell count decreases, fluctuating activity of energy metabolism-related enzymes (*e.g*., LDH) and increased DNA damage with cooling. Chang *et al*. (2016b) identified a number of genes involved in cold stress in milkfish, and noted different patterns of protein levels depending on the severity of temperature decrease [28 to 18°C (sublethal) or 16°C (lethal) at 2°C per h, then held at those temperatures]; nonlethal and lethal cold stress in the liver were typically associated with proteins mitigating oxidative and apoptosis, respectively, with higher abundances of proteins involved in maintaining immune function during nonlethal cold stress but prioritizing energy production and homeostasis (*e.g*., pH regulation) during lethal cold stress. Major changes in the expression patterns for a number of relevant genes [*e.g*., elevated *ub* (ubiquitin) in the liver, *hif2a* (hypoxia-inducing factor 2a] in the brain – see *Primary Stress Response* section) – were reported in Korean rockfish after cold shock (16 to 5°C for 12 h), though serum amino acid concentrations in cold-shocked fish remained unchanged relative to a control group (Song *et al*., 2019b). Differences in the expression of a large number of genes pertaining to energy and lipid metabolism, maintaining cellular structure and signalling pathways were identified in olive flounder (Hu *et al*., 2014). Tissue-specific variations in total gene expression in zebrafish subjected to cold stress (28 to 10°C over 48 h) have been identified by Hu *et al*. (2015). Cold-induced differences in gene expression have also been determined in larval zebrafish under several treatment regimes (28 to 16°C for 2 or 48 h; Long *et al*., 2012; 28 or 16°C to 12°C for up to 48 h; Long *et al*., 2013; 28 or 18°C to air exposure at 10°C; Long *et al*., 2015). Lyu *et al*. (2018) characterized genes implicated in the cold shock response in the livers of Korean rockfish acclimatized to 16°C and transferred directly to 5°C water for 12 h. Transcriptomic, metabolomic and proteomic differences between fugu (*Takifugu fasciatus*) exposed to 24 h cold stress (26 to 12°C following a 12 h pause at 19°C) and those kept at ambient temperature were characterized by Wen *et al*. (2019a, 2019b). A multitude of unique gene transcripts (>300,000) implicated in the cold stress (18 to 7.5°C at 1°C per h) response of yellow drum (*Nibea albiflora* Richardson 1846) have been described by Xu *et al*. (2018a). Zhou *et al*. (2019b) identified transcriptomic differences between cold-stressed (28 to 8°C over 36 h, held at 8°C for 6 h) Nile tilapia and individuals left at control temperatures, noting renal apoptosis occurring in cold-stressed fish. Transcriptional changes in response to thermal stress have even been recorded in Antarctic bullhead notothen (*Notothenia coriiceps* Richardson 1844) acclimatized to 2°C and cold shocked at −2°C (Kim *et al*., 2019). In zebrafish larvae, cold shock for 4 h (28.5 to 18°C) induced both increases and decreases in miRNA levels pertaining to genes covering wide range of functions, including cellular signalling, molecule/electrolyte transport and metabolism (Hung *et al*., 2016). A number of miRNA expression levels were likewise differentially affected over 96 h of cold shock in the head kidney tissues of GIFT tilapia (28–9.4°C; Qiang *et al*., 2018).

### 4.2.4 | Other cellular and molecular responses, osmoregulation

Other cellular and molecular responses are not as well studied in the cold shock literature. We identified one experiment in our search that focused on viability and proteomic changes in isolated fish cells following acute or gradual temperature decreases. In cultured embryonic zebrafish cells (Z4F), cold shock (28 immediately to 10°C for 24 h) induced cell death in nearly half of the cells while a more gradual temperature change (28 to 18°C for 24 h, then 18 to 10°C for 24 h) resulted in very little change in mean cell viability (Yan *et al*., 2020). Similar work may become more prevalent in the literature as more "omics" approaches to physiological stress continue to gain traction.

Low temperatures, like other stressors, may induce osmoregulatory failure and subsequent behavioural impairments in fishes, with plasma ion concentrations moving towards environmental concentrations as freshwater fish lose ions and marine fish gain ions (Donaldson *et al*., 2008). Cold acclimatization can allow for fish to resist osmoregulatory dysfunction as a result of acute temperature decreases. Buhariwalla *et al*. (2012) examined the effects of cold shock on resilience to hypotonic shock in opercular epithelial tissues from mummichogs, finding that cold shock below a certain threshold (20 to ≤5°C) caused failure for the tissues to respond to hypotonic stress. Furthermore, mummichogs acclimatized to warm (20°C) or cold (5°C) water for 4 weeks and subjected to each temperature (*i.e*., 20 to 20, 20 to

5, 5 to 20 and 5 to 5°C) showed increased membrane fluidity in the liver, and opercular epithelial tissues displayed normal responses to hypotonic shock when acclimatized and tested at 5°C, whereas those acclimatized to 20°C and tested at 5°C failed to respond normally to hypotonic shock (Buhariwalla *et al*., 2012).

In osmoconformers, some evidence suggests that low temperature stress may induce osmorespiratory compromise, wherein a trade-off is presented between ensuring adequate oxygen uptake and minimizing undesirable ion/water loss through the gills or other gas exchange sites (Gilmour & Perry, 2018). Giacomin *et al*. (2019) found that plasma osmolality decreased in Pacific hagfish (*Eptatretus stoutii* Lockington 1878) following acute temperature change (12 to 7°C), with plasma ammonia concentrations decreasing by *c*. 60% but no significant changes in other major plasma ion concentrations (*e.g*., $Na^+$ and $Cl^-$). The hagfish in Giacomin *et al*.'s (2019) experiment also exhibited different rates of change between oxygen consumption, ammonia flux and water flux across changing temperatures.

## 4.3 | Tertiary stress response

### 4.3.1 | Survival, whole-body health, development and morphometry

The survival and general performance of fish under cold stress are dependent on both the severity (*i.e*., temperature change) and duration of exposure, and tolerance to acute temperature change in general varies considerably across taxa (Donaldson *et al*., 2008). In spotted seatrout (*Cynoscion nebulosus* Cuvier 1830), fish acclimatized to 13°C and exposed to either 7, 5 or 3°C for 10 days exhibited decreasing survival with colder temperature exposures (Ellis *et al*., 2017b). Furthermore, the critical thermal minima ($CT_{min}$) of spotted seatrout was lower for fish in more saline water, whereas less saline water corresponded with higher temperatures at which individuals lost equilibrium (Ellis *et al*., 2017b). Similarly, King and Sardella (2017) reported lower $CT_{min}$ in Mozambique tilapia acclimatized to colder temperatures and in salt water over fresh water. If acclimatization is possible (*i.e*., if the magnitude of cold shock/stress is not too great), chronically cold-exposed fish may exhibit decreasing critical thermal minima, indicating higher tolerances of subsequent low temperature stress (*e.g*., Fangue *et al*., 2014). Nonetheless, critical thermal maxima ($CT_{max}$) will also tend to decrease in cold-acclimatized individuals, and thus the overall thermal tolerance range is not necessarily improved by acclimatization at cooler temperatures (di Santo & Lobel, 2017). The acclimatization of milkfish in cool (18°C) sea water resulted in lower critical thermal minima than milkfish acclimatized to warm (28°C) sea water, or either cool or warm fresh water (Kang *et al*., 2015), suggesting important interactions between temperature and physiological states associated with acclimation to other environmental characteristics.

Cold shock and stress can be lethal if fish are unable to acclimatize to or cope with temperature changes, and greater and/or more rapid temperature decreases may be more likely to result in decreasing survival rates. Winter mortality of caged gizzard shad (*Dorosoma cepedianum* Lesueur 1818) began to increase dramatically once natural temperatures fell below a threshold of *c*. 8°C (Fetzer *et al*., 2011), with laboratory experiments eliciting sharper mortality rates in more rapidly cooling tanks. GIFT tilapia mortalities steadily increased over 96 h post-transfer from 28 to 12, 11, 10, 9 or 8°C, with colder temperatures also eliciting steeper cumulative mortality rates (Qiang *et al*., 2018). Juvenile major carp acclimatized to 28°C showed mortality rates of *c*. 20%, 25%, 40% and 90% as temperatures decreased to 25, 20, 15 or 10°C, respectively at 2°C decreases per day (Sharma *et al*., 2016). In juvenile Murray cod (*Maccullochella peelii* Mitchell 1838), silver perch (*Bidyanus bidyanus* Mitchell 1838) and golden perch (*Macquaria ambigua* Richardson 1845), varying degrees of acute cold shock (23 to 19, 17, 15 or 13°C) induced higher mortality rates at larger temperature differences (Michie *et al*., 2020b). All (100%) juvenile red drum (*Sciaenops ocellatus* Linnaeus 1766) exposed to 1 or 3°C (from 8°C) died within 14 days, whereas 80% of individuals exposed to 5°C died over the same period (Anderson & Scharf, 2014). In further simulated winter cold snaps, mortality was lowest (*c*. 24%) in red drum exposed to brief, infrequent decreases from *c*. 8 to 3°C, *c*. 44% and *c*. 32% in fish exposed to brief but frequent or long but infrequent snaps, respectively, and *c*. 83% in fish exposed to long and frequent cold snaps (Anderson & Scharf, 2014). Conversely, no short-term (24 h) mortalities were observed by Hubenova and Zaikov (2013) following transfer of juvenile northern pike (*Esox lucius* L. 1758) across vastly different temperatures (the most extreme decrease being 28 to 3°C); nonetheless, water temperatures were allowed to gradually return to ambient temperatures (*c*. 13°C) over 7–8 h immediately after fish transfer, precluding long-term exposure to experimental temperatures.

Low temperature stress may worsen, or serve as the impetus for, various fish disease outbreaks, especially in aquaculture where large homogenous communities may be kept in suboptimal conditions. Cold shock (27 to 19°C for 120 h) resulted in highly accelerated mortality in orange-spotted grouper infected with the bacterial pathogen *Vibrio alginolyticus* relative to both heat-stressed (27 to 35°C) and control (held at 27°C) fish (Cheng *et al*., 2009). Goodwin *et al*. (2009) found increased incidence of cyprinid herpesvirus 2 (CyHV-2) in farmed goldfish (*Carassius auratus* L. 1758) following acute cold shock (22 to 10°C for 3 h), emulating plausible changes in temperature that cultured fish may experience during transport and shipping. Abrupt temperature decreases (12 to 8°C) in Chinook salmon (*Oncorhynchus tshawytscha* Walbaum 1792) increased susceptibility to the pathogenic bacterium *Renibacterium salmoninarum* and subsequent declines in survival 120 days later (Purcell *et al*., 2016). Elgendy *et al*. (2015) described a mass mortality event in cultured Nile tilapia attributable to severe cold stress and exacerbated by declining water quality as toxic metabolites accumulated in holding ponds, which also corresponded with an increase in pathogen abundance and diversity in deceased individuals.

Cold also tends to delay or prolong growth and development of whole individuals and specific organs/tissues (Donaldson *et al*., 2008); nonetheless, very little attention has been devoted to developmental

differences in individuals and organs/tissues as a result of acute cold shock or stress, with the bulk of the literature instead focusing on the effects of long-term cold acclimatization. Largemouth bass and smallmouth bass (*Micropterus dolomieu* Lacepède 1802) eggs exposed to acute cold or heat shocks (*c*. 17 to 10, 15, 20, 25 or 30°C, maintained throughout hatching/larval development) were generally not affected in terms of hatching success or larval survival except at the highest temperature increase, suggesting that eggs and larvae from the studied populations have some natural resilience to environmentally realistic temperature decreases (Landsman *et al*., 2011), although the authors noted that temperature changes within this range are still capable of prompting nest-guarding parental males to abandon their offspring (Suski & Ridgway, 2007). Mean survival rates of yellow perch (*Perca flavescens* Mitchill 1814) yolk-sac fry acclimatized to *c*. 11.5°C and cooled by 4 or 8°C (0.36 and 0.73°C per h, respectively) did not differ relative to an ambient control group; nonetheless, individuals in the 8°C decrease treatment displayed reversible but hazardous behavioural impairment (cessation of development, loss of swimming activity) during cold shock (VanDeHey *et al*., 2013).

From the limited investigation of cold stress effects on gill structure and morphology, Donaldson *et al*. (2008) made note of the potential for acute cold exposure to shrink gill tissues as well as the apparent lack of evidence for gill damage at the cellular level. Other cold-induced damage or alterations in tissue/organ health and development were likewise understudied; nonetheless, recent research has shed some light in this area. Following severe long-term seasonal cold stress, extensive tissue damage and necrosis were observed in Nile tilapia spleens, livers, pancreases, gills and kidneys (Elgendy *et al*., 2015). Acute temperature decrease (24 to 14°C for 24 h) resulted in the reduction of hepato-somatic index in small-scaled pacu, likely because of the mobilization of glycogen to meet cold-induced energy demands (Bacchetta *et al*., 2020). In the intestines of large yellow croaker subjected to cold stress (23 to 9°C, 1°C per h), negative impacts were observed primarily in the form of microvilli damage, likely increasing permeability with potential ramifications for elevated susceptibility to pathogen and toxin uptake (Liu *et al*., 2019b). In the same experiment, Liu *et al*. (2019b) also observed detrimental effects on liver tissues in the form of hepatocyte enlargement and cell membrane damage. Uliano *et al*. (2010) observed limited hypertrophy (cell enlargement) in cold-shocked mosquitofish (27 to 20°C) at 0‰ salinity, whereas individuals at 35‰ salinity (combined salinity and thermal stress) exhibited both hypertrophy and hyperplasia (increased cellular reproduction rates). In the same experiment, zebrafish gills at 0‰ salinity (control) exhibited slight hypotrophy (cell shrinkage) at 20°C, whereas at 25‰ salinity and 20°C (combined salinity and thermal stress) the epithelial cells became visibly detached from the basement membrane and deformed (Uliano *et al*., 2010). Mohammadi *et al*. (2019) described necrosis and epithelium detachment following acute cold shock (*c*. 22 to 4°C), and hyperplasia in lamellar tissues following 7 days of cold stress (*c*. 22 to 6°C) in Mesopotamian nase (*Chondrostoma regium* Heckel 1843). Comparing cold-tolerant and cold-sensitive olive flounders, the cold-sensitive individuals tended to have more gill damage (branchial lamellae swelling, epithelial hypertrophy and rupture) following cold stress (15 to 0.7°C, *c*. 1°C per h) than cold-tolerant individuals (Nie *et al*., 2019a).

### 4.3.2 | Swimming performance, activity and metabolic rate

Temperatures below a species' thermal tolerance ranges, or rapid decreases in temperature, can often reduce swimming activity and performance and cause reflex impairment in cases of more acute shock. In general, swimming activity and time required to exhaust fish were lower in more severely cold-shocked juvenile Murray cod, silver perch and golden perch (Michie *et al*., 2020b). Mottled mojarra (*Ulaema lefroyi* Goode 1874) acclimatized to 24°C and acutely exposed to 20, 18 or 16°C for 1 h had higher likelihoods of equilibrium loss and reflex impairment over time at 18°C and especially at 16°C (Samson *et al*., 2014). Trends in post-exposure chases to exhaustion and movement during chases were less clear, with mojarra exposed to 16°C having longer chase times than fish at 18 or 20°C and more lines crossed than fish at 18°C (despite none of these treatments differing significantly from the 24°C control; Samson *et al*., 2014). Equilibrium loss and reflex impairment are often thought of as symptoms of chemical anaesthesia (Summerfelt & Smith, 1990) and also can occur following cold stress or other debilitating stressors such as toxicity (McKim *et al*., 1987). Equilibrium loss in wild fish has obvious implications for failure to avoid predators (*e.g*., Danylchuk *et al*., 2007) or impingement against hydroelectric facility structures (McLean *et al*., 1985). Hassan *et al*. (2013) reported Nile tilapia losing equilibrium for roughly 1 h after being transferred directly from 25 to 14°C. Spotted seatrout acclimatized to 14°C lost equilibrium at *c*. 3.5°C following a 1°C per day decrease, with mortality typically occurring shortly thereafter at *c*. 3°C (Anweiler *et al*., 2014). Bonefish exposed to a 14°C temperature decrease for 2 h were more likely to lose equilibrium than fish exposed to a 7°C temperature decrease or a handling control; nonetheless, they did not differ in terms of duration or degree of movement during a subsequent chase to exhaustion (Szekeres *et al*., 2014). Swimming activity was greatly reduced within 30 min in *B. bendelisis* cold shocked (20 to 5°C) for 72 h (Kapila *et al*., 2009). Between salinities of 0 and 20‰, mosquitofish exhibited increased swimming activity rates when cold shocked at 20°C (relative to 27°C ambient temperature; Uliano *et al*., 2010). Bluegill (*Lepomis macrochirus* Rafinesque 1819) acclimatized to 22°C and acutely exposed to swimming performance tests at 14 and 18°C exhibited decreases in maximum labriform (*i.e*., primarily fin-driven) and undulatory (*i.e*., primarily body-driven) swimming speeds with respect to a control or individuals exposed to warmer water, with the temperature at which fish switched from labriform to undulatory swimming also decreasing with temperature (Jones *et al*., 2008). Similarly, Lim and Ellerby (2009) observed that the labriform swimming speed of bluegill decreased by *c*. 10 cm $s^{-1}$ following acute temperature change (22 to 14°C), coupled with a *c*. 40% decrease in $MO_2$ (Lim & Ellerby, 2009). Zebrafish larvae acclimatized to 28.5°C displayed greatly reduced

swimming speed and overall activity following 1 min exposure to 7 or 10°C and subsequent testing in ambient conditions (Lopez-Luna *et al*., 2017). Impaired critical swimming speed ($U_{crit}$) has been reported following acute cold exposure in juvenile silver perch (Parisi *et al*., 2020).

Low temperature exposure may reduce standard and maximum metabolic rates (MMR) (as measured by $O_2$ consumption). Pacific hagfish exposed to an acute temperature decrease from 12 to 7°C exhibited a significant decrease in $MO_2$ and water flow rates over the gills (Giacomin *et al*., 2019). Mohammadi *et al*. (2019) exposed Mesopotamian nase acclimatized to 21–23°C to immediate cold shock (*c*. 4°C) or cold stress (0.6°C per h to *c*. 6°C) for either 24 h or 7 days. The authors found that each cold treatment equally reduced standard metabolic rate relative to an ambient control group, whereas MMR and aerobic scope also decreased in each treatment but especially the 7 day cold stress group (Mohammadi *et al*., 2019). Nonetheless, it is not often reported whether reduced metabolic rates are the result of other stress-induced physiological changes or if they are typical, reversible consequences of temperature change alone. The latter appears to be the case in Xie *et al*.'s (2017) experiment, where the authors found that acute temperature decrease (25 to 20 or 15°C, at 0.5°C or 1°C per h, respectively) resulted in highly similar reductions in routine $MO_2$ in snakehead compared with individuals acclimatized to each temperature, despite the acclimatized fish having higher mean ventilation frequencies than cold-shocked fish. Other environmental parameters may interact with the potential impacts on cold on metabolism and internal physiological states; for instance, at salinities of 10 and 25‰, cold-shocked (27 to 20°C) zebrafish exhibited lower routine $MO_2$ whereas no such changes were observed at 0 or 20‰ salinity (Uliano *et al*., 2010). Routine $MO_2$ reductions have been observed following increases in salinity in other species, depending on their natural tolerance ranges and acclimatization histories (*e.g*., Haney & Nordlie, 1997; Hettler, 1976). Metabolic acclimatization to low temperatures is certainly possible, but the required timeframes for this have not been thoroughly studied in many species or systems. Acute exposure to cold temperatures suppressed both routine and MMR in juvenile silver perch acclimatized to 24°C and tested at 14°C, as well as $U_{crit}$, with considerable time (*c*. 7 weeks) required for metabolic acclimatization to suboptimal temperature exposure (Parisi *et al*., 2020).

### 4.3.3 | Foraging, predation and microhabitat selection

Cold shock and chronic cold stress can cause fish to reduce or even cease food intake, which has been shown more frequently in aquaculture settings (*e.g*., Ahmad *et al*., 2014; Zerai *et al*., 2010). Typically, reports of changes in feeding rates are accompanied by related changes in biomarkers pertaining to the activities or expressions of relevant proteins or genes, respectively. Acute cold stress (28 to 15°C for 24 h) greatly reduced goldfish foraging activity and food consumption (Chen *et al*., 2019b), and was related to increased leptin I and leptin II mRNA expression (which act as inhibitors of feeding activity; Yan *et al*., 2016) in the goldfish livers. Larger temperature decreases had increasingly negative impacts on food consumption rates in cold-stressed walking catfish (*Clarias batrachus* L. 1758; 25 to 20, 15 or 10°C at 2°C per day), with fish exhibiting virtually no changes in the 20°C group, food consumption decreasing with cooling and then recovering in the 15°C group, and almost total cessation of food consumption in the 10°C group (Ahmad *et al*., 2014). For all low temperature groups in that experiment, significant reductions in protease activity were reported relative to the 25°C control group (Ahmad *et al*., 2014). Periods of normal temperature punctuated by shorter but frequent cold shock episodes can likewise reduce food consumption. Gilthead seabream exposed to temperatures of 20°C (ambient) for 3 days and 12°C for 2 days over a 21 day period consumed roughly 60% of the amount consumed by a control group and had grown less by the end of the sampling period, coupled with increases in muscle oxidative capacity and mitochondrial respiration and biogenesis to cope with thermal stress (Bermejo-Nogales *et al*., 2014).

Fish may be prevented from exhibiting anti-predator behaviours by low temperature stress, although few experiments have attempted to quantify this (Donaldson *et al*., 2008). Microhabitat selection under cold stress likewise remains severely understudied. Cold shock (*c*. 29 to 24°C for 4 h) induced hyperactivity and prevented checkered puffers from successfully inflating following a simulated predation attempt (Cull *et al*., 2015). Administering a brief cold shock to larval zebrafish elicited avoidance of the darker section of a behavioural arena, which the authors deemed more likely to have occurred because of internal physiological changes affecting decision-making and microhabitat preference rather than by directly (physically) impairing swimming or sensory capabilities (Bai *et al*., 2016). Nonetheless, the physiological mechanisms underpinning cold-induced changes in microhabitat use or preference have yet to be elucidated.

### 4.3.4 | Population and community effects

Extreme cold weather events can have tangible, large-scale impacts on fish communities, particularly in warmer environments where temperature changes can be more dramatic. Hsieh *et al*. (2008) report mass mortalities following a cold snap in 183 different species from a coral reef system in the Pescadores. Fetzer *et al*. (2011) posit that gizzard shad mortalities from severe winter cold stress in northern latitudes are likely primarily driven by a failure to acclimate to the extreme cold, based on a combination of overwinter field surveys and laboratory experiments. Ellis *et al*. (2017a) revealed direct impacts of low winter temperatures on spotted seatrout survival using acoustic telemetry, where high mortality rates were reported for individuals that failed to vacate rapidly cooling areas once temperatures decreased to *c*. 5–7°C.

There are several scenarios in which cold shock can impact entire fish populations and communities. First, and most commonly, population- and community-level effects can occur when an extreme weather event causes rapid cooling over the geographic range of a

particular population or community (*e.g.*, Bohnsack, 1983). Nonetheless, populations/communities can also be affected by cold shock if they have formed in (and are sustained by) anthropogenically warmed waters and the heat source is interrupted or removed, resulting in an abrupt cooling to natural temperatures below the tolerance threshold of the population/community in question (*e.g.*, downstream of power plants releasing warmwater discharge; Masuda, 2020; see "Insight for Policymakers, Managers, and Industry Professionals" below), or from the sudden release of cold water from bottom-release dams (*e.g.*, Michie *et al.*, 2020a; Parisi *et al.*, 2020).

## 5 | INSIGHT FOR POLICYMAKERS, RESOURCE MANAGERS AND INDUSTRY PROFESSIONALS

Within a given species, populations from different geographic regions may exhibit differences in their normal physiological functions (*e.g.*, metabolic rates, growth and resistance to various types of stressors). VanLandeghem *et al.* (2013) illustrated that in the case of physiological responses to cold shock, source populations of largemouth bass from very different latitudes (*c.* 42° 20′ N *vs. c.* 30° 57′ N) can appear to respond similar to cold by some metrics (*e.g.*, plasma cortisol) but differently by others (*e.g.*, blood glucose). Therefore, management efforts focusing on protecting fish populations and communities from cold stress might be best enacted on smaller geographic scales with well-established understandings of population-specific tolerance or sensitivity to low temperature stress rather than highly generalized policies covering broad, climatically diverse regions. Another geographic consideration of cold stress and management concerns potential implications for invasive species, which have long been a serious issue in conservation science (Clavero & García-Berthou, 2005). Species-specific resilience to cold shock and cold stress can be an important consideration in assessing risk and management strategies for invasive fish populations, where differences in the thermal stress tolerances of native *vs.* invasive species could contribute to higher competitive and predatory capabilities in the invasive species (Lau *et al.*, 2019).

The release of cold water from bottom-release dams and reservoirs at hydroelectric facilities is of significant concern for fish species downstream of the release point. In China, cold effluent from increased damming of the Yangtze River is predicted to decrease water temperatures and food and prey availability, as well as delay spawning seasons of native fish (Wang *et al.*, 2020d). Similar occurrences have been documented in other systems (*e.g.*, Zhong & Power, 1996), and the problem of cold water release can be compounded by the combined effects of several dams within a singular system (*i.e.*, the so-called cascade systems; Cheng *et al.*, 2015). Hydroelectric power plants can influence both observed average downstream temperatures and the magnitude of temperature fluctuations while plants are in operation, which may negatively impact the growth and development of fishes in affected streams (Eldridge *et al.*, 2015). At a dam in Australia, an attempt to use a special "cold water curtain" to draw (and therefore release) warmer surface water inadvertently led to a cold shock event in 2020 when the apparatus failed and cold water was flushed downstream of the dam, interfering with many species' spawning seasons (Thackray, 2020). Although once-through-cooling power plants have a thermally heated discharge, cold shock may also occur if the warm wastewater release is disrupted during cold periods, leading to decreasing water temperatures until the heated discharge resumes. In 2013, cessation of warm water release occurred at a power plant in Pictou Harbour, Nova Scotia, which was associated with a large mortality event in striped bass (*Morone saxatilis* Walbaum 1792; Buhariwalla *et al.*, 2016). If power plant operators are aware of instances where warm-water discharge will be paused or interrupted during winter months, monitoring procedures should be put in place to attempt to track the potential impacts of subsequent thermal change on local fish communities. Buhariwalla *et al.* (2016) reported life-history traits (age, weight, length, *etc.*) in the dead striped bass, but a more proactive monitoring approach could also allow for the sampling of physiological stress- and cold shock-related biomarkers.

Naturally occurring temperature drops because of seiches (standing wave oscillations in a water body) are a common occurrence in the Great Lakes and other lentic systems, and have been implicated in cold shock events (*e.g.*, Emery, 1970). Thermocline disturbance and movement during seiches can lead to rapid temperature changes, particularly in shallower areas; Hlevca *et al.* (2015) reported temperature decreases of up to 15°C over a 4 h period in Toronto Harbour. A natural die-off of alewife was reported in the media on 12 August 2019 when thousands of fish were observed killed along the shoreline east of Cobourg, Ontario (Davis & Guthrie, 2019). A drastic drop in temperature (up to 15°C) was recorded by the nearby Ajax Land Ocean Biophysical Observatory (LOBO) offshore buoy data just before the die-off. Fish with impaired swimming performance because of cold stress, including those attributable to the aforementioned natural circumstances, may subsequently be impinged on the intake screens of power plants and prevented from escaping under sufficiently high flow rates, and/or killed by subsequent temperature decreases when unable to escape impingement (EPRI, 2011; Patrick *et al.*, 2015). On the contrary, temperatures likely to induce cold shock/stress and the resulting sublethal and/or lethal effects in sensitive species do occur near power plant cooling water intakes where impingement is more likely to occur (Wismer & Christie, 1987). For instance, gizzard shad (EPRI, 2011; Fetzer *et al.*, 2011) and threadfin shad (*Dorosoma petenense* Günther 1867; EPRI, 2011) tend to increase substantially once temperatures decrease to roughly 4–6°C, which can be expected in cooler parts of these species' native range. Although cold tolerance generally improves with lower acclimatization temperatures, the absolute magnitude of tolerable temperature change typically decreases with acclimatization temperature (Wismer & Christie, 1987). In other words, an acute temperature decrease might be more easily tolerated in relatively warm-acclimatized fish than in cold-acclimatized fish if final temperatures fall within tolerable limits of the warm-acclimatized fish but outside those of the cold-acclimatized fish. Comprehensive data sets on $CT_{min}$, lower incipient lethal temperature (LILT), and other

thermal stress-related endpoints have been compiled for a number of species in the Great Lakes watershed (*e.g.*, ECCC, 2019; Wismer & Christie, 1987). Thus, two important considerations when working with dead/moribund impinged fish are (a) whether fish were affected by natural cold shock events prior (and unrelated to) impingement, or were impinged while alive and unable to escape from rapid temperature decreases; and (b) understanding that fish impinged at coolant water intakes during winter seasons may be more vulnerable to cold shock than fish impinged during warmer seasons.

Coolant water inflow rates that are slower than critical swimming speeds may help in preventing or reducing impingement; nonetheless, this would only hold true for fish whose swimming capabilities have not been totally compromised by cold stress (*e.g.*, equilibrium loss; EPRI, 2011). The chances of impingement may increase with intake volume flow rates and velocities. Temperature changes as a result of power plant operating procedures (or the cessation thereof) may result in temperature changes that are too small to elicit notable thermal stress effects in fish, though attempts to quantify thermal stress must consider the taxonomic variability in thermal tolerance (and resilience) to determine which species may or may not show such effects (ECCC, 2019). Monitoring efforts geared towards impingement and cold shock relationships must also involve an ability to differentiate between fish that were killed as a result of impingement and subsequent cold shock *vs.* fish that were killed pre-impingement and enter the intake structures as moribund fish or carcasses (EPRI, 2011). Several straightforward, temperature-dependent metrics of assessing approximate times of death for impinged fish have been evaluated (*e.g.*, eye cloudiness, gill colour, extent of rigour mortis) and may be suitable for deceased impinged fish captured within the first *c.* 48 h of death (EPRI, 2011). Thus far, there have been no experimental evaluations of molecular methods of time-of-death measurement in impinged fish, such as the depletion of ATP (Korhonen *et al.*, 1990) or muscle connectin content (Seki & Watanabe, 1984) associated with rigour mortis and other post-mortem changes, which may be very useful but are likewise dependent on temperature (*e.g.*, Tomlinson *et al.*, 1961). Such metrics are generally more costly and have largely been studied in the context of seafood quality, but may allow for more precise time of death estimates over a longer period of time (Hong *et al.*, 2017).

When extreme cold weather events such as polar vortices occur, fishes capable of large-scale movements in rapidly cooling areas may attempt to disperse to warmer areas to avoid the impending sublethal and possibly lethal thermal stress (Matich & Heithaus, 2012). For fish that are unable to do so, or elect to remain in the area, the resulting cold shock can cause mass mortality events, with major potential implications for population structure and genetic diversity in fish that survive (Matich & Heithaus, 2012). The Connecticut Department of Energy and Environmental Protection posited that a winter die-off of Atlantic menhaden (*Brevoortia tyrannus* Latrobe 1802) may have been caused by a missed migration, leading more individuals to spend the winter in rapidly cooling waters (Lapinsky, 2020). Familiarity with geographic locations and connectivity between fish populations can help managers understand the impacts and likelihood of recovery following cold shock induced by extreme cold weather events, because the presence and proximity of unaffected populations may help to restore those that were impacted by the event (*e.g.*, Hsu & Gwo, 2017), and cold snaps, much like wildfires, are naturally occurring phenomena that are not inherently harmful but may become more severe/frequent as a result of climate change (Szekeres *et al.*, 2016). Bohnsack (1983) described a winter cold snap that resulted in mass mortalities in reef fish off the coast of Florida in 1977 followed by a sharp increase in species richness over the following summer, suggesting that this cold snap was a regular disturbance that helped account for the high diversity of reef fish in accordance with the intermediate disturbance hypothesis. The intermediate disturbance hypothesis, put forth by Connell (1978), essentially posits that species diversity is maximized when a system is exposed to disturbances that are frequent enough to induce substantial changes in species richness and compositions, but not so frequent as to prevent ecological succession. Indeed, cold shock events can occur frequently in areas such as Florida (*e.g.*, Brown, 2018; Milligan, 2010) and may become even more common as a result of changing weather patterns and anthropogenic climate change (Petherick, 2010; Szekeres *et al.*, 2016).

## 6 | COLD SHOCK AND FISHERIES

### 6.1 | Commercial and recreational fisheries

Fish may experience cold shock when rapidly transferred from water to colder air or to colder water in storage facilities, which can occur during routine practices in recreational and commercial fisheries. We identified only one experiment that investigated effects of cold air exposure during simulated recreational ice fishing. Prolonged exposure (5 min) to sub-freezing air temperatures (−7°C) following simulated winter angling impaired critical swimming speed (but not oxygen consumption rate) in bluegill acclimatized to *c.* 5–6°C water, whereas shorter (*c.* 30 s) exposure times and/or above-freezing temperatures had no effects on swimming speed or oxygen consumption (Bieber *et al.*, 2019). The burst swimming speeds and gill morphologies of largemouth bass exposed to the same protocols were not adversely affected by air temperatures or exposure durations. Together, these data suggest relative resilience to cold stress in bluegill and largemouth bass acclimatized to cold water; nonetheless, minimizing air exposure and handling stress remains an important welfare consideration as it is in warmer months (Bieber *et al.*, 2019). As recreational angling in winter seasons is a popular activity in North America and elsewhere, and exposure of fish to sub-freezing air temperatures during winter angling is virtually inevitable (Lawrence *et al.*, n.d.), further investigations of the welfare associated with ice fishing handling practices and cold shock are warranted.

Non-target species or fishes outside of the desirable size ranges for commercial fishing vessels frequently undergo unnecessary handling and therefore experience additional stress (Cook *et al.*, 2019). Some commercial fishing vessels practice live chilling (*e.g.*, immersing caught fish in an ice slurry) and do not sort through individuals until

they return to port after considerable time (Hyvärinen *et al*., 2004). Zander (*Sander lucioperca* L. 1758) caught by trawling and immersed directly in *c*. 0°C water (>15°C temperature decrease) for 2 h exhibited high mortality rates (*c*. 91%) compared to fish exposed to *c*. 0°C for only 10 min and a non-chilled control (*c*. 27–28%; Hyvärinen *et al*., 2008). Thus, the adoption of more efficient fish handling, sorting and release protocols that minimize handling and unnecessary stress (*e.g*., thermal shock) on vessels that use live chilling techniques is recommended. In a simulation of air exposure and temperature changes relevant to commercial fishing scenarios, little skates (*Leucoraja erinacea* Mitchill 1825) that were acclimatized to 4°C and air exposed at 1°C for 15 or 50 min exhibited decreasing blood pH and increasing blood lactate levels over time, as well as elevated blood $pCO_2$ at 50 min and mortality rates (Cicia *et al*., 2012). Although these effects on little skate welfare and survival were not as severe as those that were acclimatized to 18°C and air exposed at 27°C for the same time periods (Cicia *et al*., 2012), these results suggest that long air exposure events, acute thermal shocks and tangible lethal or sublethal impacts are not limited to hot summer months and that commercial fisheries too should endeavour to develop fish handling strategies that mitigate the combined negative effects of cold shock and air exposure on fish welfare.

## 6.2 | Aquaculture and dietary mitigation of winter stress syndrome

Winter stress syndrome (WSS), also called "winter disease" (*e.g*., Silva *et al*., 2014), refers to the predictable lethal and sublethal consequences of seasonal cold stress, and is of particular relevance to aquaculture industries as WSS accounts for significant losses of fish worldwide (Liu *et al*., 2020; Zerai *et al*., 2010). Direct mortalities can be caused by cold, but as described earlier, chronic cold stress can also have deleterious impacts on the growth and immunological function of fishes (*e.g*., Song *et al*., 2019a). Symptoms of WSS primarily include weight loss and malnourishment, decreased swimming activity and food intake, poorer immune function and other cascading sublethal (and eventually lethal) impacts of cold on fish fitness (Lemly, 1996). Many experiments since 2008 have examined the effects of supplementing cultured fish diets with a diverse array of nutrients that may be beneficial in mitigating the impacts of cold stress and cold shock on fish stress, metabolism, growth and survival. We list an overview of such experiments, the nutrient(s) investigated, study species, response(s) measured and overall results in Table 2. Note that certain considerations, such as the potential impacts of certain supplement doses on humans following fish consumption (*e.g*., nanoparticles; Parsai & Kumar, 2020), are not discussed here.

Rearing temperatures can result in a trade-off between survival and developmental rates. Réalis-Doyelle *et al*. (2016) raised brown trout (*Salmo trutta* L. 1758) from eggs at 4, 6, 8, 10 or 12°C following initial acclimatization at 8°C and reported higher long-term (>40 days) survival rates in fish reared at 4 or 6°C but with delayed development, particularly at 4°C. Saillant *et al*. (2008) provided evidence of heritable tolerance to rapid cold shock in red drum. Given the apparently substantial intraspecific variation in cold tolerance, selective breeding practices in cultured fish at risk of cold stress (*e.g*., seasonal change) may be implemented to produce fish strains that are more resilient to cold stress. For fish raised in aquaculture settings, some evidence suggests that certain euryhaline species may also be more resilient to low temperature stress when acclimatized to sea water rather than fresh water. Milkfish, for instance, appeared to benefit from acclimatization to sea water, as these fish are more prone to oxidative stress following rapid temperature decreases when acclimatized to fresh water (Chang *et al*., 2016a, 2017). Freshwater acclimatization in milkfish also led to increased glycogenolysis in the liver in attempts to meet the energy demands of cold conditions, whereas milkfish acclimatized in sea water were likely more resilient to chronic cold stress *via* an apparent shift towards lipid metabolism (Chang *et al*., 2018). Assem *et al*. (2013) investigated whether isotonic holding conditions could decrease the energetic burden of osmoregulation, thereby freeing up available energy for other essential needs. Nile tilapia that were acclimatized to fresh water and abruptly exposed to (and kept in) colder water exhibited a decrease in haemoglobin by 3 h after the acute temperature change, returning to normal levels by 6 h post-cold shock, as well as a decrease in muscle lipid content by 3 h post-exposure that remained until 168 h post-exposure, whereas no such changes were observed in fish acclimatized to isotonic water (Assem *et al*., 2013). Using a similar protocol, Hassan *et al*. (2013) observed Nile tilapia cold shocked (from 25 to 14°C) in isotonic water exhibited increases in blood glucose and decreases in gill ATPase and brain acetylcholinesterase activity that were less pronounced and shorter than cold-shocked tilapia in fresh water. Optimal rearing salinities may be as important as optimal temperatures in ensuring the survival of cultured fish; nonetheless, much more work on other species and systems is required before more specific conclusions can be drawn.

## 6.3 | Cold shock as a fisheries science and management tool

Acute cold shock can be used to induce androgenesis or gynogenesis (inheritance of solely male or female genetic material, respectively), as well as polyploidy, in fish. Triploidy may be induced using cold to interfere with meiosis II, allowing retention of the second polar body in a fertilized egg (Felip *et al*., 2001). In places where WSS is particularly problematic, some evidence suggests triploid fish may be less resilient to low temperature stress than their diploid counterparts across a wide range of acclimatization temperatures. Saranyan *et al*. (2017) report lower HSP70, HSP90, heat shock factor 1 (HSF1) and free and total ubiquitin protein levels in triploid Atlantic salmon and brook charr (*Salvelinus fontinalis* Mitchill 1814) relative to their diploid conspecifics following a 100 day acclimatization period (16 to 6°C). Nonetheless, we are unaware of any experimental evaluations of whole-organism resilience to acute cold shock between conspecific triploids and diploids. Androgenesis and gynogenesis have traditionally used combinations in fertilization from irradiated sperm

**TABLE 2** Effects of various diet supplementations on fish responses to cold shock/stress relative to non-supplemented control groups

| Reference | Species | Added nutrient | Response | General effects against cold stress |
|---|---|---|---|---|
| Bacchetta *et al.* (2020) | Small-scale pacu (*Piaractus mesopotamicus*) | β-carotene (105.1 mg $kg^{-1}$) | Blood glucose | Mitigated effects of acute cold shock on blood glucose |
| Ge *et al.* (2020) | Large yellow croaker (*Larimichthys crocea*) | APSH-07 (≥30 mg $kg^{-1}$) | Blood glucose | Mitigated effects of acute cold shock on blood glucose |
| Castro *et al.*, 2012 | Senegalese sole (*Solea senegalensis*) | Dietary protein (45 or 55%) | Antioxidant enzyme activity (SOD, CAT, GPx, G6PDH, LPO) | Higher dietary protein generally improved resilience to oxidative stress following cold shock |
| Chuang and Sun Pan (2011) | Mozambique tilapia (*Oreochromis mossambicus*) | *Glycine tomentella* root extract (1%) | Blood viscosity | Root extract reduced blood viscosity following acute cooling |
| Wang *et al.* (2020c) | Mozambique tilapia (*O. mossambicus*) | Resveratrol (25 mg $kg^{-1}$) | Oxygen consumption: nitrogen excretion ratio | Prevented reduction with low temperature stress |
| Abdel-Ghany *et al.* (2019) | Nile tilapia (*Oreochromis niloticus*) | Corn oil (4%), coconut oil (4%), fish and corn oil mix (2% and 2%) | Survival | Fish and corn oil mix resulted in relatively higher tolerance for low temperatures |
| Toutou *et al.* (2019) | Nile tilapia (*O. niloticus*) | *Salvadora persica* stem powder (0.25, 0.5 or 1%) | Survival | Stem powder slightly reduced mortality, but high variation observed in the data |
| de Araújo *et al.* (2017) | Nile tilapia (*O. niloticus*) | Spray-dried plasma (16.6, 33.2, 49.7 or 66.3 g $kg^{-1}$) | Haematocrit, white and red blood cell counts and other haematological parameters | Variable effects of spray-dried plasma on cold stress response |
| Li *et al.* (2018) | Nile tilapia (*O. niloticus*) | Chromium picolinate (0.6, 1.2 or 1.8 mg $kg^{-1}$) | Serum triiodothyronine (T3), creatine kinase and cortisol | Supplemented diets corresponded with higher T3 and lower creatine kinase and cortisol levels following cold stress |
| Wu *et al.* (2019b) | Nile tilapia (*O. niloticus*) | *Astragalus membranaceus* extract (0, 0.1, 0.2 or 0.4% diet mass) | Survival, growth rate, serum cholesterol and cortisol, antioxidant enzyme activity | Supplementation generally improved survival and growth rate and lowered cholesterol and cortisol, but had variable impacts on antioxidant enzyme activity following cold stress |
| Pezeshk *et al.* (2019) | Electric yellow cichlid (*Labidochromis caeruleus* Fryer 1956) | Red, green or brown algae extracts (*Gracilaria persica*, *Entromorpha intestinalis* and *Sargassum boveanum*) (1 g $kg^{-1}$) | Survival | Supplemented diets improved post-cold shock survival, most notably in green algae *E. intestinalis*-supplemented fish |
| Lee *et al.* (2017) | Orange-spotted grouper (*Epinephelus coioides*) | Sodium alginate (1000 mg $kg^{-1}$) | Serum cortisol, glucose, lactate; bacterial infection | Sodium alginate mitigated changes in serum parameters and reduce susceptibility to infection following cold stress |
| Luo *et al.* (2014) | Orange-spotted grouper (*E. coioides*) | Fatty acid-binding protein 10 (1%) | Muscle ATP availability; antioxidant enzyme activity | FABP10 improved ATP supply and antioxidant enzyme activity following cold stress |
| Luo *et al.* (2015a) | Orange-spotted grouper (*E. coioides*) | $\alpha_2$-macroglobulin receptor (1%) | Immune function (blood cell counts, antioxidant enzyme activity) | Improved general immune response to cold shock |
| Luo *et al.* (2015b) | Orange-spotted grouper (*E. coioides*) | *Dissostichus mawsoni*-Calmodulin (1%) | Immune function (blood cell counts, antioxidant enzyme activity) | Improved general immune response to cold shock |

**TABLE 2** (Continued)

| Reference | Species | Added nutrient | Response | General effects against cold stress |
|---|---|---|---|---|
| Ye *et al.* (2016) | Obscure pufferfish (*Takifugu obscurus*) | Monocalcium phosphate (0.6–0.8% P content) | Blood cell counts, antioxidant enzyme activity, long-term growth | Improved resistance to viable blood cell count depression following acute cold shock, and promoted antioxidant enzyme activity and long-term growth |
| Cheng *et al.* (2018a) | Obscure pufferfish (*T. obscurus*) | Taurine (250, 550, 850, 1140, 1430 or 1740 mg $kg^{-1}$) | Antioxidant gene activity, ROS production, apoptosis | Some variable concentration-dependent effects on antioxidant gene expression, and decrease in ROS production and apoptosis frequency at higher doses under low temperature stress |
| Cheng *et al.* (2018b) | Obscure pufferfish (*T. obscurus*) | Vitamin C (2.6, 48.9, 95.5, 189.8, 382.4 or 779.5 mg $kg^{-1}$) | ROS production, apoptosis, DNA damage | Variable concentration-dependent effects ROS production, apoptosis frequency and DNA damage under low temperature stress |
| Saavedra *et al.* (2010) | White seabream (*Diplodus sargus* L. 1758) | Phenylalanine (20 g $kg^{-1}$) or phenylalanine and tyrosine (10 and 47 g $kg^{-1}$) | Survival | Higher survival in tyrosine-supplemented diets following acute cold shock |
| Seiedzadeh *et al.* (2016) | Binni (*Mesopotamichthys sharpeyi* Günther 1874) | Chicken egg lecithin (2–6%) | Survival | Higher survival rates in lecithin-fed group following 24 h cold shock |
| Soltanian *et al.* (2014) | Iridescent striped catfish (*Pangasianodon hypophthalmus*) | β-glucan (0.5, 1 or 2%) | Serum cortisol, survival | No effects on cortisol; survival improved following 24 h cold shock in 0.5%–1% groups |
| Kumar *et al.* (2017a) | Iridescent shark catfish (*P. hypophthalmus*) | Selenium nanoparticles (1 mg $kg^{-1}$) | $CT_{min}$, $LT_{min}$ | Supplemented diets corresponded with lower $CT_{min}$ and $LT_{min}$ |
| Kumar *et al.* (2017b) | Iridescent shark catfish (*P. hypophthalmus*) | Zinc nanoparticles (10 or 20 mg $kg^{-1}$) | $CT_{min}$, $LT_{min}$ | Supplemented diets corresponded with lower $CT_{min}$ and $LT_{min}$ |
| Kumar *et al.* (2018a) | Iridescent shark catfish (*P. hypophthalmus*) | Zinc acetate (10 or 20 mg $kg^{-1}$) | $CT_{min}$, $LT_{min}$ | Supplemented diets corresponded with lower $CT_{min}$ and $LT_{min}$ |
| Kumar *et al.* (2019) | Iridescent shark catfish (*P. hypophthalmus*) | Selenium nanoparticles and riboflavin (5, 10 or 15 mg $kg^{-1}$) | $CT_{min}$, $LT_{min}$ | Supplemented diets corresponded with lower $CT_{min}$ and $LT_{min}$ relative to stressed, but not unstressed, conspecifics |
| Kumar *et al.* (2018b) | Striped snakehead (*Channa striata*) | Silver nanoparticles (0.5 mg $kg^{-1}$) | $CT_{min}$, $LT_{min}$ | Supplemented diets did not correspond with lower $CT_{min}$ and $LT_{min}$ |
| Lu *et al.* (2019a) | Zebrafish (*Danio rerio*) | α-lipoic acid (0.6 g $kg^{-1}$) or reduced glutathione (0.3 g $kg^{-1}$) | Total liver antioxidant capacity, liver antioxidant enzyme activity, apoptosis/inflammation gene expression, survival | Following cold stress, α-lipoic acid improved total antioxidant capacity, both diets increased CAT activity and improved survival and generally decreased apoptosis/inflammation-related gene expression |
| Lu *et al.* (2019b) | Zebrafish (*D. rerio*) | Fenofibrate (6.67 g $kg^{-1}$) | Survival | Addition of fenofibrate improved survival following cold shock |

*Note*: Note that other considerations (*e.g.*, human health aspect of fish consumption) were not accounted.

and cold shock (Chen *et al*., 2017; Manan *et al*., 2022); nonetheless, recent developments allow androgenesis to occur without radiation by extrusion of female nuclei along with the second polar body (Morishima *et al*., 2011). A list of cold shock-induced genetic modifications in fish that appeared in our literature search is provided in Table 3.

The intentional chilling of live fish has been investigated in the contexts of aquaculture and anaesthesia/euthanasia. Zeng *et al*. (2014) reported ≥70% survival in crucian carp (*Carassius carassius* L. 1758) that had been exposed to acute temperature decreases from 18 to 0°C and then stored live outside of water at 4 or 0°C. Nonetheless, the overall absence of research focusing on the welfare of live fish

**TABLE 3** List of genetic modifications (*e.g*., androgenesis and polyploidy) achievable in various fish species *via* cold shock, from literature published since 2008

| Modification | Species | Reference |
|---|---|---|
| Androgenesis | Japanese pufferfish (*Takifugu rubripes* Temminck & Schlegel 1850) | Zhou *et al*., 2019a |
| | Olive flounder (*Paralichthys olivaceus* Temminck & Schlegel 1846) | Hou *et al*., 2016 |
| | Pond loach (*Misgurnus anguillicaudatus* Cantor 1842) | Hou *et al*., 2013; Morishima *et al*., 2011; Zhou *et al*., 2018b |
| Gynogenesis | Zebrafish (*Danio rerio* Hamilton 1822) | Hou *et al*., 2015 |
| | Asian stinging catfish (*Heteropneustes fossilis* Bloch 1794) | Anusha & Marx, 2012 |
| | Bagrid catfish (*Pelteobagrus ussuriensis* Dybowski 1872) | Pan *et al*., 2017 |
| | Blunt snout bream-topmouth culter hybrids (*Megalobrama amblycephala* × *Culter alburnus* Basilewsky 1855) | Wu *et al*., 2019a |
| | Blunt-snout bream (*M. amblycephala* Yih 1955) | Gong *et al*., 2019 |
| | Common carp (*Cyprinus carpio* L. 1758) | Xiao *et al*., 2011 |
| | Grass carp (*Ctenopharyngodon idella* Valenciennes 1844) | Mao *et al*., 2019; Zhang *et al*., 2011 |
| | Half-smooth tongue sole (*Cynoglossus semilaevis* Günther 1873) | Chen *et al*., 2009 |
| | Japanese pufferfish (*T. rubripes* Temminck & Schlegel 1850) | Zhang *et al*., 2013 |
| | Large-scale loach (*Paramisgurnus dabryanus* Dabry de Thiersant 1872) | You *et al*., 2008 |
| | Olive flounder (*P. oilvaceus* Temminck & Schlegel 1846) | Liu *et al*., 2013; Ma *et al*., 2018; Wang *et al*., 2020a |
| | Senegalese sole (*Solea senegalensis* Kaup 1858) | Molina-Luzón *et al*., 2015 |
| | Ship sturgeon (*Acipenser nudiventris* Lovetsky 1828) | Hassanzadeh Saber & Hallajian, 2014; Hassanzadeh Saber *et al*., 2014 |
| | Spotted halibut (*Verasper variegatus* Temminck & Schlegel 1846) | Ji *et al*., 2010 |
| | Stellate sturgeon (*Acipenser stellatus* Pallas 1771) | Hassanzadeh Saber *et al*., 2008 |
| | Turbot (*Scophthalmus maximus* L. 1758) | Nie *et al*., 2019b; Xu *et al*., 2008 |
| | Walking catfish (*Clarias batrachus* L. 1758) | Marx, 2011 |
| | Wels catfish (*Silurus glanis* L. 1758) | Fopp-Bayat, 2010 |
| | Yellow drum (*Nibea albiflora* Richardson 1846) | Chen *et al*., 2017 |
| Triploidy | African catfish (*Clarias gariepinus* Burchell 1822) | Hammed *et al*., 2010; Karami *et al*., 2010; Normala *et al*., 2016, 2017 |
| | Black sea turbot (*Scophthalmus maeoticus* Pallas 1814) | Aydın & Okumuş, 2017 |
| | Brown trout (*Salmo trutta* L. 1758) | Preston *et al*., 2013 |
| | Grass puffer (*Takifugu niphobles* Jordan & Snyder 1901) | Hamasaki *et al*., 2013 |
| | Nibe croaker (*Nibea mitsukurii* Jordan & Snyder 1900) | Takeuchi *et al*., 2018 |
| | Olive flounder (*P. oilvaceus* Temminck & Schlegel 1846) | Liu *et al*., 2018b; Xu & Chen, 2010 |
| | Red tilapia (*Oreochromis mossambicus* × *O. niloticus*) | Pradeep *et al*., 2012, 2013, 2014 |
| | Senegalese sole (*S. senegalensis* Kaup 1858) | Molina-Luzón *et al*., 2015 |
| | Silver catfish (*Rhamdia quelen* Quoy & Gaimard 1824) | García *et al*., 2017; Morón-Alcain *et al*., 2017 |
| | Spotted sand bass (*Paralabrax maculatofasciatus* Steindachner 1868) | Alcántar-Vázquez *et al*., 2008, 2016 |
| | Yellowtail tetra (*Astyanax altiparanae* Garutti & Britski 2000) | Adamov *et al*., 2017 |
| | Zebrafish (*D. rerio* Hamilton 1822) | Franěk *et al*., 2019; van de Pol *et al*., 2020 |
| Alloploidy | Hybrid loaches (*M. anguillicaudatus* × *P. dabryanus*) | Huang *et al*., 2017; Huang *et al*., 2018 |
| Tetraploidy | Pond loach (*M. anguillicaudatus* Cantor 1842) | Fujimoto *et al*., 2010 |

preservation and transport in cold waterless environments is concerning, and limited current evidence does not lend support to this practice. Even with fish kept in water, there is a paucity of evidence on which to base recommendations for/against the live chilling of popular commercial and hatchery fish species such as Atlantic salmon (Foss *et al*., 2012). Turbot, chilled in sub-zero sea water, exhibit signs of physiological stress such as osmoregulatory failure and experience uncontrollable muscle contractions (Roth *et al*., 2009). Hypothermia has been investigated as a possible means of anaesthesia; nonetheless, equilibrium loss, reflex impairment and other behavioural signs of apparent "unconsciousness" belie evidence that suggests hypothermia has no consistently reliable anaesthetic or analgesic effect (*e.g*., Lambooij *et al*., 2015). Low temperatures may be used to slaughter (or assist with the slaughter of) fish in aquaculture; nonetheless, hypothermia has also been regarded as a controversial method of euthanasia in a number of jurisdictions (Wilson *et al*., 2009) as it does little to minimize the stress response or potentially adverse conscious experience of fish being euthanized by this method over a relatively long time compared to other available methods (*e.g*., electrical stunning and physical methods; Lambooij *et al*., 2006). Immersion in ice water took far longer to euthanize common carp than high $CO_2$ exposure or clove oil overdose (Rahmanifarah *et al*., 2011), whereas ice water immersion was faster at euthanizing matrinxã than $CO_2$ (Vargas *et al*., 2013). Time-to-euthanasia differences may be attributable to interspecific variation in thermal stress tolerance. In places where food fish are slaughtered *via* electric stunning, cold shock has also been used to ensure that fish do not recover following exposure to the electric current (Grimsbø *et al*., 2014), and so hypothermia may only be suitable as a means of preventing recovery following the administration of a more effective, humane euthanasia technique.

## 7 | METRICS FOR QUANTIFYING COLD STRESS IN FISH

In Table 4, we present a list of metrics that are potentially suitable for quantifying cold shock/stress in fish. They refer readers to Sopinka *et al*. (2016) for detailed descriptions of diverse indicators of stress in a broader context (including available methodologies as well as more thorough descriptions of the advantages and disadvantages associated with each metric). It is important to note that each of these is to some degree susceptible to confounding/interacting stressors and may change only if the rate and/or magnitude of temperature decreases or exceeds a certain threshold. Moreover, quantifying higher numbers of individual responses, such as enzyme activities, for a particular facet of cold stress (*e.g*., oxidative stress, energy mobilization and immune function) can provide a broader understanding of how various physiological responses link together than measuring one or two. In the case of oxidative stress, researchers can quantify potential damage (*e.g*., ROS and TBARS levels), antioxidant enzyme activity (*e.g*., SOD and CAT) or antioxidant enzyme production/gene expression; nonetheless, each of these may exhibit different response patterns that, taken together, provide deeper insight into the physiology of cold-induced oxidative stress. For instance, not all antioxidant enzymes respond the same way to cold stress over a given timeframe and such changes are also likely to differ across tissues (*e.g*., Joy *et al*., 2017). Similarly, certain well-established metrics of cold stress (*e.g*., HSPs) may not respond to cold stress in predictable manners if transcription activity is already elevated by temperature or other stressors (Borchel *et al*., 2017).

Given the lack of research on catecholamine and neuroendocrine responses to cold in the last *c*. 12 years, cortisol measured in blood plasma or serum is currently the most reliable primary stress biomarker for quantifying cold shock/stress in fish. Moreover, cortisol is related to and interacts with many other elements of the generalized stress response (*e.g*., immune function and energy mobilization; Baker *et al*., 2013) and is therefore useful in accompanying other metrics. Nonetheless, it is increasingly recognized that cortisol is not just a "stress hormone" and indeed plays other roles in organism function (MacDougall-Shackleton *et al*., 2019) which are worthy of study in terms of the influence of cold shock on fish. In terms of secondary stress markers, apparent inconsistencies across multiple unrelated experiments such as changes (or lack thereof) in blood glucose or blood cell counts may be attributable to different species, study systems and temperature changes, but to differentiate between the relative contributions of these factors requires more comprehensive works that attempt to piece together the "big picture" within a single experiment/study system. This need for comprehensive, integrative approaches applies to tertiary stress markers as well, particularly those that have received little attention to date (*e.g*., behaviour, population- and community-level effects of cold shock/stress). Establishing behavioural effects such as changes in movement patterns in experimental arenas is useful, but would benefit from the concurrent study of potential physiological explanations for observed behaviours leading to better predictive value and applicability of results. Thus, the optimal approach to quantifying cold shock in fish involves the use of multiple relatable metrics that represent primary, secondary and/or tertiary stress responses. The interactions between various stress indicators and the implications for their measurement have been reviewed extensively by others (*e.g*., Baker *et al*., 2013; Sopinka *et al*., 2016). Nonetheless, attempting to link physiological stress markers across multiple scales, from molecular responses to whole-body health and fitness to population level effects, has gradually gained recognition as a useful practice in conservation science (Bergman *et al*., 2019), and may also be useful to the cold shock literature as knowledge gaps between metric interactions are slowly bridged.

Researchers must also consider *a priori* knowledge about the thermal tolerance and resilience of species of interest when designing experiments or conducting field studies on potential cases of natural or anthropogenic cold shock (*i.e*., is a particular rate/magnitude of temperature decrease sufficiently large and biologically relevant in inducing physiological stress?). For instance, migratory fishes that may be exposed to cold stress during natural migration movements may be particularly well adapted to mitigating cold stress through changes in gene expression that help maintain normal biological functions (Wang *et al*., 2020b). Gene expression is also subject to seasonal variation, as

**TABLE 4** Summary of common primary, secondary and tertiary stress responses used to quantify cold stress

| Stress response category | Biomarker/metric | Source/level of response | Utility for quantifying cold shock/stress | Advantages/disadvantages (based on Sopinka *et al.*, 2016) | Example species and references |
|---|---|---|---|---|---|
| Primary | Cortisol, corticosteroids | Blood<br>Organs/tissues<br>Whole-body<br>Excreted waste | Well-established metric of physiological stress, but visible changes may be delayed by cold temperatures, or might only be visible at certain magnitudes or rates of temperature change | Advantages: Suitable for direct measures of stress and can be used to quantify acute and chronic stress with respect to baseline values<br>Disadvantages: Responses must often be characterized for different species/strains | *Micropterus salmoides* (VanLandeghem *et al.*, 2010)<br>*Lophiosilurus alexandri* (Mattioli *et al.*, 2020) |
| Secondary | Glucose | Blood | May indicate changes in energy demand/mobilization, best accompanied by more reliable/consistent metrics (*e.g.*, cortisol) | Advantages: Easy to measure, provides insight on physiological processes relating to energy mobilization<br>Disadvantages: Can be influenced by other factors (*e.g.*, diet), best for acute stress | *Sphoeroides testudineus* (Cull *et al.*, 2015)<br>*Chanos chanos* (Chang *et al.*, 2020) |
| | Lactate | Blood | May be influenced by unrelated muscle activity and should accompany more reliable/consistent metrics (*e.g.*, cortisol) | Advantages: Easy to measure, provides insight on exercise and physical exertion<br>Disadvantages: Can be influenced by other factors (*e.g.*, unrelated movement activity), best for acute stress | *Albula vulpes* (Szekeres *et al.*, 2014)<br>*C. chanos* (Chang *et al.*, 2020) |
| | Osmolality, osmorespiratory function | Blood | Changes in osmolyte concentrations may be observed following cold shock; pair with osmorespiratory enzyme function and gene expression to better understand mechanisms of change | Advantages: Osmoregulatory failure and/or changes in relative ion concentrations can follow acute stress<br>Disadvantages: Can be influenced by other environmental factors and physiological processes | *Fundulus heteroclitus* (Buhariwalla *et al.*, 2012)<br>*Eptatretus stoutii* (Giacomin *et al.*, 2019) |
| | Red blood cells (counts, haematocrit, *etc.*) | Blood | Haematocrit is generally a poor cold stress indicator | Advantages: Easy to measure and can reflect oxygen transport in the blood<br>Disadvantages: Can change sporadically or inconsistently in response to stress | *Scophthalmus maximus* (Ji *et al.*, 2016)<br>*Piaractus mesopotamicus* (Bacchetta *et al.*, 2020)<br>*L. alexandri* (Mattioli *et al.*, 2020) |
| | White blood cells (counts, leucocrit, *etc.*) | Blood | Leucocrit is generally a poor cold stress indicator, but changes in white blood cell counts may be better indicators than red blood cells; specific white blood cell counts may be measured as a proxy of immune function | Advantages: Easy to measure and reflective of health and immune function<br>Disadvantages: Pre-existing stress, diseases, *etc.* can confound measurements | *S. maximus* (Ji *et al.*, 2016)<br>*P. mesopotamicus* (Bacchetta *et al.*, 2020)<br>*L. alexandri* (Mattioli *et al.*, 2020) |
| | Heat and cold shock proteins (HSPs, CSPs, *etc.*) | Blood<br>Various tissues | Expression and activities of HSP/CSP tend to reflect the magnitude and severity of cold stress; nonetheless, changes in particular proteins tend to be species- and tissue-specific and therefore likely require validation | Advantages: Generally reliable, and functions for many individual HSPs are well established<br>Disadvantages: History/degree of stressor exposure and acclimation can alter HSP response patterns | *Cyprinus carpio* (Ali *et al.*, 2010)<br>*Siniperca chuatsi* (He *et al.*, 2019) |

**TABLE 4** (Continued)

| Stress response category | Biomarker/metric | Source/level of response | Utility for quantifying cold shock/stress | Advantages/disadvantages (based on Sopinka *et al.*, 2016) | Example species and references |
|---|---|---|---|---|---|
| | Oxidative stress markers (GPx, GST, CAT, SOD, *etc.*; ROS) | Various tissues | Measuring multiple antioxidants and/or ROS can be a reliable indicator of oxidative stress from cold shock | Advantages: Important stress biomarker directly relatable to individual fitness costs<br>Disadvantages: Responses are complicated by various biological processes affecting oxidative stress markers | *Amphiprion melanopus* (Park *et al.*, 2011)<br>*Etroplus suratensis* (Joy *et al.*, 2017) |
| | Lipid concentrations, metabolism (relevant gene expression, protein activity, *etc.*) | Various tissues | Changes in protein activities or gene expression implicated in lipid metabolism may serve as indicators of energy demands associated with cold shock/stress | Advantages: Can provide relevant insight into individual health over short and long timescales<br>Disadvantages: Do not always respond consistently to stress across individuals, stressors | *Paralichthys olivaceus* (Hu *et al.*, 2014)<br>*O. niloticus* (He *et al.*, 2015) |
| | [a]Visible cell/tissue damage, cell death | Blood<br>Various tissues | Best measured alongside more fine-scale metrics (*e.g.*, LDH activity, apoptosis-related mRNA expression) to quantify degrees of tissue damage | Advantages: Easy to measure and can provide evidence of physical impacts of cold stress<br>Disadvantages: Lethal sampling may be required to sample certain tissues | *O. niloticus* (Zhou *et al.*, 2019b)<br>*Gambusia affinis*, *Danio rerio* (Uliano *et al.*, 2010) |
| | [a]"Omics" (genomics, proteomics, metabolomics, *etc.*) | Blood<br>Various tissues<br>Whole-body | Large-scale characterization of genes involved in cold shock/stress responses can provide considerable insight between and within species (including cold tolerant *vs.* cold sensitive individuals) | Advantages: Provides comprehensive, large-scale understanding of stress-induced physiological changes<br>Disadvantages: Responses must typically be characterized for each species/strain of interest and are not guaranteed to be consistent | *C. chanos* (Chang *et al.*, 2016b)<br>*Larimichthys polyactis* (Liu *et al.*, 2020) |
| Tertiary | Swimming activity (*e.g.*, $U_{crit}$), impairment, equilibrium loss (*e.g.*, $CT_{min}$); foraging, food intake | Individuals | Cold induces impaired changes in swimming activity and reflex impairment, and can lead to equilibrium loss; consistent with physiological changes that can be reported concurrently (*e.g.*, digestive enzyme activity) | Advantages: Provides insight on real-world consequences of cold shock/stress, with implications for predation or predator avoidance and other critical behavioural functions<br>Disadvantages: Difficult to elucidate underlying physiological mechanisms for observed behaviours | *Barilius bendelisis* (Kapila *et al.*, 2009)<br>*Cynoscion nebulosus* (Anweiler *et al.*, 2014)<br>*Clarias batrachus* (Ahmad *et al.*, 2014)<br>*Carassius auratus* (Chen *et al.*, 2019b) |
| | Metabolic rate ($MO_2$, MMR, *etc.*) | Individuals | Various measures of metabolic rate (resting, maximum, *etc.*) are intrinsically related to temperature and thermal stress | Advantages: Can be an indicator of the metabolic burden associated with stress<br>Disadvantages: Highly subject to influence from interindividual variation, environmental confounds and interacting stressors | *Bidyanus bidyanus* (Parisi *et al.*, 2020)<br>*F. heteroclitus* (Healy *et al.*, 2017) |
| | Survival/mortality | Individuals<br>Populations<br>Communities | Sufficiently rapid/dramatic temperature decreases can cause death, yet survival/mortality alone does not indicate what specific complication(s) led to death | Advantages: Most direct method of assessing lethal endpoints because of cold stress<br>Disadvantages: Can be influenced by other confounding factors (*e.g.*, disease, unrelated stressors), and alone does not provide insight into sublethal effects | *Dorosoma cepedianum* (Fetzer *et al.*, 2011)<br>*Labeo catla* (Sharma *et al.*, 2016) |

[a]Not precisely/individually described by Sopinka *et al.* (2016).

certain cold-induced genes (*e.g.*, those associated with the production of glycerol or antifreeze proteins) may play a role in acclimatizing to colder temperatures in both warm- and cool-water fish (*e.g.*, Ammar *et al.*, 2018; Barat *et al.*, 2012). Accounting for potential pre-existing thermal stress (*e.g.*, if collecting wild fish during or shortly after extreme weather) and ensuring appropriate time frames are important considerations, especially as various genes and other stress metrics implicated in both cold stress and acclimatization may require different amounts of time to show either phase in a readily distinguishable manner.

Further research into "omics" (genomics, proteomics, *etc.*) approaches would also provide a greater selection of available metrics for quantifying cold stress. Akbarzadeh *et al.* (2018) reviewed and identified a number of genes whose activity could be measured in various tissues from several salmonid species, primarily in response to high temperature stress (*e.g.*, SERPINH1, COX6B1). A similar synthesis focusing on genetic responses to low temperature stress would greatly benefit researchers looking to quantify cold shock using genetic biomarkers that may be identifiable with genome-wide techniques (*e.g.*, Xu *et al.*, 2018a). Other potential biomarkers or metrics of assessing the impacts of low temperature stress on fish and fish populations require further study on the breadth and scope of their applications, reliability and relationships with other metrics, before more concrete recommendations can be made. For instance, primary stress biomarkers such as catecholamine release tend to respond to stress over very short timeframes and may be very difficult to measure in field studies or complex laboratory experiments (Sopinka *et al.*, 2016). Precise impacts of cold on both predation and anti-predator behaviours are still understudied, though these are also intrinsically related to other tertiary measures of stress including swimming activity, reflex impairment and general performance.

## 8 | REVIEW LIMITATIONS

Our literature search results were limited to works published no earlier than 2008 and written in English (although "All languages" was selected in our Web of Science Core Collections search, any non-English results were subsequently excluded). The subject of this review is of interest at a global scale, and there may be works in the non-English primary literature that are not cited here. The issue of language barriers is also true for grey literature sources, which may be less widely accessible (*e.g.*, technical reports from industry and government). By searching for English results only in the FSL, we may have missed Canadian grey literature written in French. There was also uneven representation of the various countries in which experiments and studies were conducted. The countries that contributed the highest numbers of articles were China (82 of 239), the United States (25), Taiwan (17) and India (16). The remaining articles described work conducted in 33 other countries (detailed in Appendix S2). Given the volume of works conducted in regions where English is not a primary language, it is plausible that these regions may have many other pertinent primary or grey literature works in their native languages that were not accessible in our searches.

The evidence base showed a paucity of peer-reviewed field studies on natural cold shock events (five articles detailed marine field studies, and only one article described a combined field study and experiment in fresh water). Field studies from both systems, but especially fresh water, are therefore underrepresented in this review. The lack of field studies may be explained by a lack of active monitoring for such events despite the fact that in many circumstances they may be expected or predictable (*e.g.*, seasonal die-offs). Included articles focused almost exclusively on ray-finned fish (Actinopterygii), which comprised 250 (including 4 artificial hybrid species) of the 254 represented taxa in the included articles. The most commonly represented species were typically of high interest to aquaculture and fisheries, or as small model species for laboratory work [*e.g.*, zebrafish (20 articles), Nile tilapia (15), olive flounder (11) and orange-spotted grouper (10)]. Other taxa, particularly those that are of little or no interest to aquaculture and fisheries, are underrepresented in the literature despite the fact that natural cold shock events impact fish communities and ecosystems indiscriminately. A full description of the taxonomic classes, families and species represented in our search results is included in Appendix S2.

## 9 | CONCLUSIONS AND FUTURE RESEARCH PRIORITIES

Considerable progress has been made since Donaldson *et al.*'s (2008) review on cold shock in fish; nonetheless, many of the major knowledge gaps remain partially or fully unaddressed. Donaldson *et al.* (2008) highlighted the need for an investigation of the primary stress response at the preliminary level, comprising catecholamine release and other brain responses that occur before the release of cortisol and subsequent impacts on secondary and tertiary stress markers. Some experiments have shed light on the effects of cold shock/stress and immune function, with implications for whole-organism fitness and resilience to other stressors such as diseases (*e.g.*, Cheng *et al.*, 2009), though often there are no established causal relationships between secondary immune parameters and sublethal and lethal effects at the whole-organism level. The relationships between changes in biochemical processes (*e.g.*, antioxidant enzyme production and activity) and corresponding effects on the health and function of tertiary responses still require significant research investment, particularly concerning the larger-scale tertiary responses (*i.e.*, population- and community-level effects). Furthermore, the behavioural aspects of the tertiary stress response (*e.g.*, foraging/anti-predator behaviour) are likewise too understudied to permit anything beyond broad-scale generalizations without special regard for variations across taxa and systems, which is a driving theme in the complexity of cold stress/shock responses in fish.

Notably, we are unaware of any experiments or studies in the cold stress literature that link physiological biomarkers of stress to whole-organism fitness and population-level effects. Although

challenging, this molecules-to-populations approach has been used in many studies from the discipline of conservation physiology (reviewed in Bergman *et al*., 2019) and would be of tremendous benefit in improving the understanding of the generalized stress response in fish following cold shock/stress. In the absence of sufficient information on the population- and community-level impacts of cold stress and their underlying causes at the level of primary and secondary stress responses, conservation and management authorities may have difficulties in taking any form of effective action to protect fishes from cold stress, particularly in cases of cold shock that arise from anthropogenic sources (*e.g*., dam discharge) that are easier to address than extreme weather events and climate change.

There are several available tools and metrics available for researchers to quantify cold stress, summarized in the previous section and Table 4. Nonetheless, given the substantial variation in how different species respond to cold stress, what degrees of cold stress are most relevant/likely to be encountered in nature and other context-dependent factors (*e.g*., intraspecific/strain variation in cold stress tolerance), it seems generally advisable that biologically and ecologically relevant cold stress responses be characterized on a case-by-case basis in pilot projects before longer-term monitoring or experiments are carried out. One ideal approach would be to undertake a series of experiments wherein fish are exposed to realistic cold shock conditions reflecting temperature data from previous recorded cold snaps: using multiple cohorts of fish, changes in various stress response metrics following cold shock (*e.g*., cortisol, glucose and other blood chemistry parameters; HSP activity; DNA microarray analyses) can be quantified over a time course equal to or greater than the relative frequency of monitoring for impinged carcasses. Cortisol, glucose, lactate and other responses can be easily obtained *via* blood sampling from one sub-set of individuals at various time points, whereas tissue-specific gene expression and protein activities can be quantified by killing a different sub-set of fish (undergoing the exact same experimental procedure) at the same timepoints. Ideally, this practice of concurrent measurement of each response would provide insight not only on how individual responses change, but to what extent they may interact and be reflective of each other. In general, inconsistent changes in various responses appear to be especially conspicuous in secondary stress responses (*e.g*., blood metabolite profiles and HSP expression/activity), and more comprehensive approaches measuring multiple stress biomarkers at the primary, secondary and/or tertiary level are recommended (*e.g*., Ahmad *et al*., 2014). Key future research priorities include further development and characterization of "omics" approaches to quantifying cold shock; linking changes in primary, secondary and tertiary responses *via* underlying mechanisms; fundamental/immediate responses to cold shock (*e.g*., neuroendocrine responses); population- and community-level effects of cold shock (particularly for natural cold snaps or *in situ* cold shock resulting from anthropogenic causes) and establishing reliable indicators for differentiating between cold shock/stress and subsequent acclimatization processes. Together, the above considerations will aid researchers in finding optimal approaches to quantifying cold stress in both field and laboratory settings, which in turn will have implications for better welfare practices in fisheries research, wildlife management and power industries.

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## AUTHOR CONTRIBUTIONS

P.P. and S.J.C. provided ideas, supervision and direction on the project. C.H.R., J.J.T. and T.R. organized literature search protocols and performed literature searches. C.H.R. performed article screening and primary manuscript preparation. B.R., J.J.T., P.P., S.J.C., T.R. and W.G.W. further contributed to manuscript preparation and provided invaluable feedback throughout. We acknowledge the support of the Natural Sciences and Engineering Research Council of Canada (NSERC).

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