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On the neglected cold side of climate change and what it means to fish

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ABSTRACT: Over the past decade nearly all of the research on the effects of climate change on fish has focused on the effects of warmer water temperatures. Yet, it is expected that temperature variability will also increase, resulting in more frequent incidences of rapid decreases in water temperatures (i.e. cold shock). Cold shock events have caused large-scale fish mortalities, and sublethal impacts are also known to occur but are less well documented. We argue that cold shock will become an important selective force in climate change scenarios. There is a rich history of research on cold shock in the context of industrial cooling effluents and aquaculture, providing a foundation upon which to develop and extend future work on cold shock and climate change. To understand the diverse effects climate change may have on fish populations, future research needs to expand beyond the projected increases in water temperatures to include consideration of variability in temperature and the potential for cold shock.

KEY WORDS: Climate change · Water temperature · Cold shock · Fish · Research agenda

1. INTRODUCTION

For ectothermic organisms such as fishes, water temperature is regarded as the 'master factor' (Brett 1971), controlling and limiting (Fry 1971) many aspects of biology from intra-cellular metabolic processes (e.g. enzyme function) to whole organism activities (e.g. feeding, locomotion and reproduction). It is therefore not surprising that in the face of anthropogenic climate change, there is much concern about how elevated water temperatures (and other associated environmental effects such as ocean acidification; see Kelly & Hoffmann 2012) will affect fish (reviewed in Roessig et al. 2004, Ficke et al. 2007, Pörtner & Farrell 2008) and aquatic ecosystems (Hofmann & Todgham 2010, Meyer-Rochow 2013). Research on the effects of rising water temperatures has expanded in recent years with many researchers shaping their entire research programs around the consequences of a warmer climate on fish biology, ecology and evolutionary processes. While most climate change research focuses on climate warming, it is anticipated that temperature variability will also increase (Solomon et al. 2007), which gives rise for the potential of increased 'cold shock' events. Cold shock is the term to describe the stress response that occurs when a fish has been acclimated to a specific water temperature range and is subsequently exposed to a rapid decrease in temperature, resulting in a cascade of physiological and behavioural responses

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(Donaldson et al. 2008). Many factors influence the consequences of cold shock (briefly reviewed below and in Donaldson et al. 2008), and the magnitude of the response is affected by the rate of temperature decrease and the magnitude of change in relation to population-specific thermal tolerance limits and the acclimation history at the individual level.

Here we argue that the 'cold side' of climate change as it relates to fish has been neglected. Our objective is to stimulate the research community to think more broadly and consider not only the increase in temperature, but also the consequences of increased temperature variability and cold shock.

2. THE COLD SIDE OF CLIMATE CHANGE

Commonly, climate change is considered in the context of mean rise in temperatures (Hughes 2000, Pörtner et al. 2001). However, severe weather anomalies are also projected to increase in both the frequency and magnitude of events (Solomon et al. 2007, IPCC 2012). Recent research has shown that these acute variations can have more severe consequences than climate warming (Clusella-Trullas et al. 2011, Paaijmans et al. 2013, Vasseur et al. 2014). Additionally, these abrupt and often extreme weather events can act as a strong selective pressure, resulting in considerable changes to populations (Parmesan et al. 2000, Jentsch et al. 2007, Parker et al. 2008).

Climate change also has the potential to affect the frequency, extent and severity of natural occurrences of sudden cold events. Projected changes to the climate system include changes in precipitation regimes, reductions in Arctic sea ice cover, decreases of spring snow cover in the Northern Hemisphere and increased temperature variability (IPCC 2014). These climate-related changes can influence natural sources of cold events (e.g. seiches), thermoclines (e.g. depth and stability), solar heat exposure and seasonal or diel temperatures (Emery 1970, Overstreet 1974, Steiner & Olla 1985, Larimore 2002, Szekeres et al. 2014, Hlevca et al. 2015). For example, several abiotic factors may play a role in weather anomalies, including El Niño-Southern Oscillation, Eurasian snow cover, solar activity and the Quasi Biannual Oscillation (Cohen et al. 2007, Fletcher & Kushner 2011, Mitchell et al. 2011; reviewed in Kim et al. 2014). Weakening of the stratospheric polar vortex and subsequent negative phases of the Arctic Oscillation (AO) has been linked to the loss of Arctic sea ice cover (Kim et al. 2014). The negative phase of AO results in colder surface temperatures throughout the Northern Hemisphere (Kim et al. 2014), causing southward advection of Arctic air (Wang et al. 2010). If the AO continues in its negative phase, there is an increased likelihood of more frequent cold fronts of higher magnitudes, resulting in more abrupt cold events (Wang et al. 2010).

Cold shock events can have catastrophic effects on local fish populations. Weather-induced cold shock events resulting in large-scale fish mortalities in the subtropics were first documented in 1940 (Galloway 1941), with another severe event occurring in 1977 (Gilmore et al. 1978, Roberts et al. 1982, Bohnsack 1983). More recently, in January 2010, Florida recorded their coldest 12 d period since 1940 (NOAA 2010). This cold shock event resulted in the deaths of hundreds of thousands of nearshore fishes and broader impacts on coral and marine mammals (FWCC 2010, Hallac et al. 2010, Lirman et al. 2011, Adams et al. 2012, Colella et al. 2012, A. Adams [Bonefish and Tarpon Trust] pers. comm.). In 2010, a cold shock was the cause of a massive fish kill in the Bolivian reaches of the Amazon River which was considered serious enough to merit coverage as a news item in the journal 'Nature' (see www.nature.com/news/2010/100827/full/news.2010.437.html). The consequences of cold shock events are likely to vary substantially across aquatic ecosystems. Fish in tropical and subtropical systems may be most susceptible to cold shock events, as these regions have relatively little seasonal variation in daylight hours and temperatures, or diel temperature variation; thus fish are not well-adapted to temperature variations (Knutson et al. 2010, Clusella-Trullas et al. 2011). It can be speculated that fish inhabiting shallow or nearshore systems are more likely to experience cold shock events, as they may be unable to move into deeper or more stable waters given small home range sizes, and also need to avoid predators (Smythe & Sawyko 2000).

3. A PRIMER ON COLD SHOCK AND FISH

Cold shock results in a physiological stress response manifested by primary, secondary, and tertiary responses (Mazeaud et al. 1977, Donaldson et al. 2008). As water temperature decreases rapidly away from a fish's acclimation temperature, a neuroendocrine response is initiated at the central nervous system and hypothalamic-pituitary-interrenal (HPI) axis, beginning the primary response. A rapid temperature change is associated with a decrease in cerebral blood volume (CBV) (Van den Burg et al. 2005), which may be an adaptive means of limiting the flow of cold blood from the gills to the brain but has the cost of reducing the flow of oxygen-rich blood. Rapid cooling reduces the reliability of synaptic transmission and of cellular and network responses which can affect tertiary outcomes such as the predatory escape response (Preuss & Faber 2003). In response to cold shock, the HPI axis triggers a release of corticosteroid and catecholamine hormones that are correlated with the magnitude of temperature decrease from acclimation temperatures (Tanck et al. 2000).

The primary stress responses cascade into secondary responses, which include cellular, metabolic, and osmoregulatory changes. Both standard metabolic rate and maximum metabolic rate decrease with cooling temperatures, resulting in reduced scope for activity (Fry 1947). Similarly, enzyme activity rates, heart rate, and muscle power output are all reduced at cold temperatures (Hochachka & Somero 1984, Johnston & Clarke 1990, Shiels et al. 2006, Van den Burg et al. 2006) and many metabolic and osmoregulatory secondary responses have been well studied following cold shock (e.g. Datta et al. 2002, Zarate & Bradley 2003, Lermen et al. 2004). Cellular and molecular responses may be promising indicators of cold shock stress. For example heat shock proteins (HSPs), a family of stress proteins that act as molecular chaperones to protect the cell against denatured proteins during stress are known to play a role in responses to temperature stress, though there is considerable variability in HSP response to cold shock (Zakhartsev et al. 2005). Furthermore, it is well known that exposure to cold causes an increase in the amount of unsaturated membrane fatty acids and subsequent changes in ionic regulation, which can then affect muscle fibre performance and neuronal function (Meyer-Rochow 2013). A number of recent molecular genetics studies have focused on responses to temperature stress, although many of these studies have looked at increasing temperatures rather than decreasing temperatures or cold shock in particular (Somero 2012). Of the studies that have focused on gene expression in response to cold shock, thousands of genes have been found to be cold-sensitive, suggesting that there is need for future research in this area (Ju et al. 2002, Gracey et al. 2004, Gracey 2007).

Tertiary responses refer to stress on individuals as a whole (Mazeaud et al. 1977). Cold shock stress can result in impaired immune function, increased occurrence of disease, and poor health (Engelsma et al. 2003, Tierney et al. 2004, Tilney & Hocutt 1987, Black et al. 1991). Development rates are reduced during cold temperatures and in response to cold shock, and increased mortality can occur (Tang et al. 1987, Hubert & Gern 1995). Cold shock stress is associated with impaired reflexes, including reduced response to manual stimulation of the caudal region (Samson et al. 2014), impaired ventilation rates, and reduced swimming ability (Szekeres et al. 2014); factors that could affect predator evasion and foraging behaviours.

4. HISTORICAL PERSPECTIVE

Previous research on cold shock in fish has become pertinent again given the potential for cold shock events to become more common. The physiological response of fish to cold shock has been studied in a variety of fish species from a comparative as well as from an evolutionary perspective (reviewed in Donaldson et al. 2008). However, the greatest amount of work on cold shock has been in the context of 2 applied issues, in order to (1) understand the consequences of industrial thermal effluent dynamics on wild fish populations, and (2) exploit knowledge of cold shock to refine fish production in aquaculture.

In the former case, research began in the 1950s and 1960s when various industrial processes began to use water from adjacent waterbodies for cooling in industrial applications (e.g. coal or nuclear electricity generation, steel production, food processing), such that effluents were warmed above ambient conditions. Fish would be attracted to the warm effluent and, when cooling was not required, water temperatures would rapidly drop exposing fish to cold shock. These industrial scenarios where fish become acclimated to warmer temperatures and then face sudden cold shock are analogous to events that could occur in the context of storms or extreme weather events associated with climate change. The body of research related to industrial processes (reviewed in Coutant & Brook 1970, 1973) yielded various industry and government technical reports but is rarely reported in the primary literature. Some important outputs from that work include identifying species, life-stage and size-specific rates of body temperature change in fish relative to different exposures (e.g. Spigarelli et al. 1977, Weller et al. 1984) and characterizing the absolute temperature differential that caused sublethal physiological and behavioural alterations across a range of temperatures (Coutant & Brook 1970). The latter was particularly relevant for identifying what became known as Δ-Ts: the acceptable rate of change (both in terms of absolute change and the period over which the change occurred) in cooling that was permitted by regulators. Failure of water users to adhere to such regulations would result in legal action. The Δ-Ts generated for a variety of freshwater, estuarine and coastal marine fish are highly relevant today for understanding which cold shock scenarios may have sublethal or lethal consequences for wild fish. Cold shock knowledge was also useful for informing the siting of cooling systems, so that they could be placed in regions that were less likely to negatively affect fish populations (Coutant 1977). Unfortunately, climate change is less discriminating (i.e. not site specific like an effluent) but the same approach could be used to characterize the potential risk on a spatial basis (e.g. risk mapping). Although cooling loops are still in use today, their use in natural systems accessible to wild fish populations has decreased due to improvements in efficiency, such that Δ-Ts are lower and thus cold shock is less common. This is coupled with the fact that many systems now create artificial reservoirs for use in cooling. Thus, since the early 1990s there has been relatively little research on cold shock in the context of cooling loops.

In the context of fish culture, cold shock has been used for decades to induce polyploidy (i.e. individuals that contain >2 paired sets of chromosomes — most commonly triploid in the case of fish). In the 1970s and 1980s there was extensive work on a range of species to identify the conditions (thermal and otherwise) under which polyploidy would be induced. A clear theme that emerged was extensive interspecific variation and the importance of timing (reviewed in Pandian & Koteeswaran 1998). To that end, in the context of climate change, it is reasonable to conclude that not all species will have the same likelihood of polyploidy when exposed to a given level and duration of cold shock. Moreover, the timing of the cold shock relative to development seems particularly important (Piferrer et al. 2003), such that one could develop stage-specific risk criteria. It is unclear the extent to which polyploidy is or could occur in the wild as a result of cold shock, given that most of the research on the topic has been done with a decidedly culture-based focus. The other aspect of fish culture research on cold shock relevant to climate change is simply work done with the intention of identifying thresholds for temperature management in culture facilities (e.g. Barton & Peter 1998). Although direct inferences cannot be drawn about wild populations from studies of farmed fish, the general patterns and principles likely apply.

5. PUTTING COLD SHOCK RESEARCH BACK ON THE AGENDA

Given that cold shock events are likely to become more common in an era of anthropogenic climate change, there is need for more research on this topic. Indeed, there is a major bias in the literature and contemporary research, with a focus on warming waters in response to the narrative that climate change is manifested as global warming. Our purpose in writing this article is to remind the scientific community that climate change is not solely about warming, but also about increases in thermal variability. To that end, we call on the research community to expand thermal biology studies focused on climate change to include aspects of cold shock.

We have identified a number of critical knowledge gaps in cold shock research and we suggest some essential research needs to aid in filling these gaps (Table 1). Research efforts would be best focused on fish populations that reside in locations where cold shock events are most likely to occur. To that end, models need to be developed to estimate the frequency, severity and extent of cold anomalies on a site-specific basis. Because the impact of cold shock events depends on the rate of decrease in temperature and the magnitude of change relative to population-specific thermal tolerance, having the ability to predict, project and/or quantify these events would be most useful for ensuring that research efforts are most relevant. Cold shock research on its own would be useful; however, it would be particularly relevant to address aspects of both warming and thermal variability (i.e. leading to cold shock risk) within the same studies. It is our hope that in the coming years many of the research needs identified here (Table 1) will be addressed, so that the 'cold side' of climate change is given the prominence it needs in order to understand the full suite of possible consequences of climate change. In addition to individual behavioural and physiological consequences to cold shock, we encourage future research to consider community interactions. We submit that exploring the relationships between predators, competitors, and prey is fundamental to gain a more holistic understanding of ecosystem-wide consequences of cold shock events. There is also a need for research on parasitism and immune function in the face of cold shock (see Le Morvan et al. 1998 for review on immune function and temperature in fish). While earlier industrial effluent and aquaculture research forms a basis for understand-

Table 1. Suggested research agenda and corresponding research needs for an improved understanding of the potential effects of cold shock on wild fish in an era of human-induced climate change. Ideas here are specific to climate change. We direct authors to Donaldson et al. (2008) for a more generic list of mechanistic research needs for cold shock

Research agenda	Research needs
• Develop models that inform on the location, frequency, severity and extent of cold anomalies in climate, or some estimation of how increased variability will influence these parameters	• To focus research efforts on priority locations with ecological relevance
• Determine how performance and fitness-related traits are influenced by environmental variability, including both warm and cold shock events	• To focus on understanding the full suite of possible consequences of climate change (warm and cold) on individual fish
• Determine how the optimal thermal window for a given trait changes across a range of relevant fish acclimation temperatures	• To address a number of key questions including: How is the lower end of the spectrum impacted? Does the optimal thermal 'window' get narrower with increasing acclimation temperature? If so, does it get narrower as fast as the acclimation temperature increases? It may be possible to identify trait- and species-specific lower-end temperature thresholds that would vary with acclimation temperature
• Examine the ability of fish to sense and avoid incoming storms or cold shock events	• Necessary given potential for behavioural avoidance in some systems which could mitigate physiological consequences
• Determine the relative resilience of predators and prey, and competition among species in the face of cold shock	• If predators are more resilient, this may represent an opportunity for them and increased predation risk for prey; competitors may also have a similar advantage
• Determine how cellular, molecular, physiological and metabolic parameters respond as part of the cold shock response, including an emphasis on critical thermal minima and scope for activity at lower temperatures	• These factors influence how an individual copes with a cold shock event, as well as the capacity to leave/avoid cold water prior to death, or avoid predators
• Quantify the potential for longer-term, carry-over effects on fish that survive cold shock, as well as how cold shock interacts with other stressors	• Needed to understand the long-term consequences of cold shock on fitness to inform population models
• Identify the factors that influence inter-individual and intra-specific variation in response to cold shock, such as body size, development stage, disease burden, nutritional state, antioxidant capacity, and maturation state	• To standardize approaches in an effort to facilitate comparisons across studies, environments, and species
• Explore how orientation, navigation and other cognitive functions are influenced by cold shock	• To determine how behavioural decisions could be affected by cold shock

ing the effects of cold shock on fish, there are differences between these sources of cold shock from those in the context of climate change. For example, the ability of fish to sense and avoid incoming storms (Heupel et al. 2003), a major cause of cold shock in the wild, will ultimately determine their degree of vulnerability. Nevertheless, this past research forms a logical starting point to develop specific research projects and study designs that are relevant to understanding and predicting the effects of climate change on wild fish.

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LITERATURE CITED

Adams AJ, Hill JE, Kurth BN, Barbour AB (2012) Effects of a severe cold event on the subtropical, estuarinedependent common snook, *Centropomus undecimalis.* Gulf Caribb Res 24:13–21

Barton BA, Peter RE (1982) Plasma cortisol stress response in fingerling rainbow trout, *Salmo gairdneri* Richardson, to various transport conditions, anaesthesia, and cold shock. J Fish Biol 20:39–51

Black MC, Millsap DS, McCarty JF (1991) Effects of acute temperature change on respiration and toxicant uptake by rainbow trout, *Salmo gairdneri* (Richardson). Physiol Zool 42:336–357

Bohnsack JA (1983) Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal fish kill. Environ Biol Fishes 9:41–53

Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am Zool 11:99–113

Clusella-Trullas S, Blackburn TM, Chown SL (2011) Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. Am Nat 177:738–751

Cohen J, Barlow M, Kushner PJ, Saito K (2007) Stratosphere–troposphere coupling and links with Eurasian land surface variability. J Clim 20:5335–5343

Colella MA, Ruzicka RR, Kidney JA, Morrison JM, Brinkhuis VB (2012) Cold-water event of January 2010 results in catastrophic benthic mortality on patch reefs in the Florida Keys. Coral Reefs 31:621–632

Coutant CC (1977) Cold shock to aquatic organisms: guidance for power plant siting, design, and operation. Nuclear Safety 18:329–342

Coutant CC, Brook AJ (1970) Biological aspects of thermal pollution. I. Entrainment and discharge canal effects. Crit Rev Environ Sci Technol 1:341–381

Coutant CC, Brook AJ (1973) Biological aspects of thermal pollution. II. Scientific basis for water temperature standards at power plants. Crit Rev Environ Sci Technol 3: 1–24

Datta T, Acharya S, Das MK (2002) Physiological effect of cold shock in juvenile *Labeo rohita* (Hamilton–Buchanan). Indian J Fish 49:223–227

Donaldson MR, Cooke SJ, Patterson DA, MacDonald JS (2008) Cold shock and fish. J Fish Biol 73:1491–1530

Emery AR (1970) Fish and crayfish mortalities due to an internal seiche in Georgian Bay, Lake Huron. J Fish Res Board Can 27:1165–1168

Engelsma MY, Hougee S, Nap D, Hofenk M, Rombout JHWM, van Muiswinkel WB, Lidy Verburg–van Kemenade BM (2003) Multiple acute temperature stress affects lecucocyte populations and antibody responses in common carp, *Cyprinus carpio* L. Fish Shellfish Immunol 15:397–410

Ficke AD, Myrick CA, Hansen LJ (2007) Potential impacts of global climate change on freshwater fisheries. Rev Fish Biol Fish 17:581–613

Fish and Wildlife Conservation Commission (2010) Snook cold kill report. Fish and Wildlife Research Institute, St. Petersburg, FL

Fletcher CG, Kushner PJ (2011) The role of linear interference in the annular mode response to tropical SST forcing. J Clim 24:778–794

Fry FEJ (1947) Effects of the environment on animal activity. University of Toronto Studies in Biological Series 55, Publication 68, Ontario Fisheries Research Laboratory, Whitney

Fry FEJ (1971) The effect of environmental factors on the physiology of fish. Fish Physiol 6:1–98

Galloway JC (1941) Lethal effect of the cold winter of 1939–40 on marine fishes at Key West, Florida. Copeia 1941:118–119

Gilmore RG, Bullock LH, Berry FH (1978) Hypothermal mortality in marine fishes of south-central Florida, January 1977. NE Gulf Sci 2:77–97

Gracey AY (2007) Interpreting physiological responses to environmental change through gene expression profiling. J Exp Biol 210:1584–1592

Gracey AY, Fraser EJ, Li W, Fang Y and others (2004) Coping with cold: an integrative, multitissue analysis of the transcriptome of a poikilothermic vertebrate. Proc Natl Acad Sci USA 101:16970–16975

Hallac D, Kline J, Sadle J, Bass S, Ziegler T, Snow S (2010) Preliminary effects of the January 2010 cold weather on flora and fauna in Everglades National Park. Biological Resources Branch, South Florida Natural Resources Center, Everglades and Dry Tortugas National Parks, Homestead, FL

Heupel MR, Simpfendorfer CA, Hueter RE (2003) Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. J Fish Biol 63:1357–1363

Hlevca B, Cooke SJ, Midwood JD, Doka SE, Portiss R, Wells M (2015) Characterization of water temperature variability within a harbour connected to a large lake. J Great Lakes Res 41:1010–1023

Hochachka PW, Somero GN (1984) Biochemical adaptation. Princeton University Press, Princeton, NJ

Hofmann GE, Todgham AE (2010) Living in the now: physiological mechanisms of response to climate change. Annu Rev Physiol 72:127–145

Hubert WA, Gern WA (1995) Influence of embryonic stage on survival of cutthroat trout exposed to temperature reduction. Prog Fish-Cult 57:326–328

Hughes L (2000) Biological consequences of global warming: Is the signal already apparent? Trends Ecol Evol 15: 56–61

IPCC (2012) Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

IPCC (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5:365–374

Johnston IA, Clarke A (1990) Cold adaptation in marine organisms [and Discussion]. Philos Trans R Soc B 326: 655–667

Ju Z, Durham RA, Liu Z (2002) Differential gene expression in the brain of channel catfish (*Ictalurus punctatus*) in response to cold acclimation. Mol Genet Genomic 268: 87–95

Kelly MW, Hofmann GE (2012) Adaptation and the physiology of ocean acidification. Funct Ecol 27:980–990

Kim BM, Son SW, Min SK, Jeong JH and others (2014) Weakening of the stratospheric polar vortex by Arctic sea-ice loss. Nat Commun 5:4646

Knutson TR, McBride JL, Chan J, Emanuel K and others (2010) Tropical cyclones and climate change. Nat Geosci 3:157–163

Larimore RW (2002) Temperature acclimation and survival of smallmouth bass fry in flooded warmwater streams.

Am Fish Soc Symp 32:115–122
Le Morvan C, Troutaud D, Deschaux P (1998) Differential effects of temperature on specific and nonspecific immune defences in fish. J Exp Biol 201:165–168
Lermen CL, Lappe R, Crestani M, Vieira VP and others (2004) Effect of different temperature regimes on metabolic and blood parameters of silver catfish (*Rhamdia quelen*). Aquaculture 239:497–507
Lirman D, Schopmeyer S, Manzello D, Gramer LJ and others (2011) Severe 2010 cold-water event caused unprecedented mortality to corals of the Florida reef tract and reversed previous survivorship patterns. PLOS ONE 6: e23047
Mazeaud MM, Mazeaud F, Donaldson EM (1977) Primary and secondary effects of stress in fish: some new data with a general review. Trans Am Fish Soc 106:201–212
Meyer-Rochow VB (2013) Thermal pollution: general effects and effects on cellular membranes and organelles in particular. In: Allodi S, Nazari EM (eds) Exploring themes on aquatic toxicology. Research Signpost, Trivandrum, p 1–34
Mitchell DM, Gray LJ, Charlton-Perez AJ (2011) The structure and evolution of the stratospheric vortex in response to natural forcings. J Geophys Res 116:D15100, doi: 10.1029/2011JD015788
NOAA (National Oceanic and Atmospheric Administration) (2010) National Data Buoy Center. www.ndbc.noaa.gov/N (accessed 29 Sep 2015)
Overstreet RM (1974) An estuarine low-temperature fish-kill in Mississippi, with remarks on restricted necropsies. Gulf Res Rep 4:328–350
Paaijmans KP, Heinig RL, Seliga RA, Blanford JI, Blanford S, Murdock CC, Thomas MB (2013) Temperature variation makes ectotherms more sensitive to climate change. Glob Change Biol 19:2373–2380
Pandian TJ, Koteeswaran R (1998) Ploidy induction and sex control in fish. Hydrobiologia 384:167–243
Parker BR, Vinebrooke RD, Schindler DW (2008) Recent climate extremes alter alpine lake ecosystems. Proc Natl Acad Sci USA 105:12927–12931
Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bull Am Meteorol Soc 81:443–450
Piferrer F, Cal RM, Gómez C, Bouza C, Martí P (2003) Induction of triploidy in the turbot (*Scophthalmus maximus*). II. Effects of cold shock timing and induction of triploidy in a large volume of eggs. Aquaculture 220:821–831
Pörtner HO, Farrell AP (2008) Physiology and climate change. Science 322:690–692
Pörtner HO, Berdal B, Blust R, Brix O and others (2001) Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). Cont Shelf Res 21:1975–1997
Preuss T, Faber DS (2003) Central cellular mechanisms underlying temperature-dependent changes in the goldfish startle–escape behaviour. J Neurosci 23:5617–5626
Roberts HH, Rouse LJ, Walker ND, Hudson JH (1982) Cold-water stress in Florida Bay and northern Bahamas: a product of winter cold-air outbreaks. J Sediment Res 52: 145–155
Roessig J, Woodley C, Cech J Jr, Hansen L (2004) Effects of global climate change on marine and estuarine fishes and fisheries. Rev Fish Biol Fish 14:251–275
Samson E, Brownscombe JW, Cooke SJ (2014) Behavioural and reflex responses of mottled mojarra *Eucinostomus lefroyi* (Gerreidae) to cold shock exposure. Aquat Biol 23:101–108
Shiels HA, Paajanen V, Vornanen M (2006) Sarcolemmal ion currents and sarcoplasmic reticulum Ca^{2+} content in ventricular myocytes from the cold stenothermic fish, the burbot (*Lota lota*). J Exp Biol 209:3091–3100
Smythe AG, Sawyko PM (2000) Field and laboratory evaluations of the effects of 'cold shock' on fish resident in and around a thermal discharge: an overview. Environ Sci Policy 3:225–232
Solomon SD, Qin D, Manning M, Chen Z and others (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
Somero GN (2012) The physiology of global change: linking patterns to mechanisms. Annu Rev Mar Sci 4:39–61
Spigarelli SA, Thommes MM, Beitinger TL (1977) The influence of body weight on heating and cooling of selected Lake Michigan fishes. Comp Biochem Physiol A 56: 51–57
Steiner WW, Olla BL (1985) Behavioural responses of prejuvenile red hake, *Urophycis chuss*, to experimental thermoclines. Environ Biol Fishes 14:167–173
Szekeres P, Brownscombe JW, Cull F, Danylchuk AJ and others (2014) Physiological and behavioural consequences of cold shock on bonefish (*Albula vulpes*) in The Bahamas. J Exp Mar Biol Ecol 459:1–7
Tanck MWT, Booms GHR, Eding EH, Wendelaar Bonga SE, Komen J (2000) Cold shocks: a stressor for common carp. J Fish Biol 57:881–894
Tang J, Bryant MD, Brannon EL (1987) Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. Prog Fish-Cult 49:167–174
Tierney KB, Stockner E, Kennedy CJ (2004) Changes in immunological parameters and disease resistance in juvenile coho salmon (*Oncorhynchus kisutch*) in response to dehydroabietic acid exposure under varying thermal conditions. Water Qual Res J Canada 39:175–182
Tilney RL, Hocutt CH (1987) Changes in epithelia of *Oreochromis mossambicus* subjected to cold shock. Environ Biol Fishes 19:35–44
van den Burg EH, Peeters RR, Verhoye M, Meek J, Flik G, Van der Linden A (2005) Brain responses to ambient temperature fluctuations in fish: reduction of blood volume and initiation of a whole-body stress response. J Neurophysiol 93:2849–2855
van den Burg EH, Verhoye M, Peeters RR, Meek J, Flik G, Van der Linden A (2006) Activation of a sensorimotor pathway in response to a water temperature drop in a teleost fish. J Exp Biol 209:2015–2024
Vasseur DA, DeLong JP, Gilbert B, Greig HS and others (2014) Increased temperature variation poses a greater risk to species than climate warming. Proc R Soc B 281: 20132612
Wang C, Liu H, Lee SK (2010) The record breaking cold temperatures during the winter of 2009/2010 in the Northern Hemisphere. Atmos Sci Lett 11:161–168
Weller DE, Anderson DJ, DeAngelis DL, Coutant CC (1984) Rates of heat exchange in largemouth bass: experiment and model. Physiol Zool 57:413–427
Zakhartsev M, De Wachter B, Johansen T, Pörtner HO, Blust R (2005) Hsp70 is not a sensitive indicator of thermal limitation in *Gadus morhua*. J Fish Biol 67:767–778
Zarate J, Bradley TM (2003) Heat shock proteins are not sensitive indicators of hatchery stress in salmon. Aquaculture 223:175–187

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