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The role of temperature in the capture and release of fish

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Abstract

We searched major electronic databases to identify peer-reviewed literature investigating the role of temperature on the stress response and mortality of captured and released fish. We identified 83 studies that fit these criteria, the majority of which were conducted in North America (81%) on freshwater fish (76%) in the orders Perciformes (52%) and Salmoniformes (28%). We found that hook-and-line fisheries (65% of all studies) were more commonly studied than all net fisheries combined (24%). Despite the wide recognition for many species that high water temperatures exacerbate the effects of capture on released fish, this review is the first to quantitatively investigate this problem, finding that warming contributed to both mortality and indices of stress in 70% of articles that measured each of those endpoints. However, more than half (58%) of the articles failed to place the experimental temperatures into a biological context, therefore limiting their broad applicability to management. Integration of survival and sublethal effects to investigate mechanisms of fish mortality was relatively rare (28%). Collectively, the results suggest that capture–release mortality increases at temperatures within, rather than above, species-specific thermal preferenda. We illustrate how knowledge of ecologically relevant high temperatures in the capture and release of fish can be incorporated into management, which will become increasingly important as climate change exerts additional pressure on fish and fisheries.

Keywords By-catch, catch and release, climate change, discards, fishing, temperature

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Introduction

Globally, commercial fishers capture and release approximately 7 million tonnes of fish per year (Kelleher 2005), and as many as 19 million tonnes (30 billion fish) per year are estimated to be captured and released from recreational fisheries (Cooke and Cowx 2004). Fish are released because they may have little or no commercial value, they are not of the desired size, legislation prohibits their retention because the species or population is threatened, or in some recreational fisheries, release is mandated to maintain population characteristics of an unexploited population (Redmond 1986; Ross 1997). Regardless of fishing method or motivation for releasing captured fish, a capture-and-release event commonly consists of multiple separate stressors, including encountering the gear (physical injury), struggling to become free (strenuous exercise), barotrauma (fish caught at depth), human handling (potential further injury, mucous and scale loss, fear response and struggling) and air exposure (oxygen deprivation and collapse of gill structures) (Arlinghaus 2007). Sublethal effects of these stressors include altered blood chemistry, behavioural impairments, depressed growth and reproductive rates and increased vulnerability to disease (Wendelaar Bonga 1997; Barton 2002). Mortality from these stressors has been examined for multiple gear types and species and varies from 0 to 100% of released fish (Alverson *et al.* 1994; Bartholomew and Bohnsack 2005).

While a number of factors can influence post-release mortality, such as species and gear type (Chopin and Arimoto 1995; Bartholomew and Bohnsack 2005), decades of research have revealed that water temperature plays an important but complex role in post-release survival. Indeed, temperature has long been termed the ‘master factor’ in the biology of fishes for its governance over physiological processes (Brett 1971). Being ectotherms, many fish have a relatively narrow range of temperatures in which they are able to thrive, grow and reproduce (Elliot 1981). When environmental (and thus body) temperatures are elevated above the optima for a particular species, fish may exhibit abnormal behaviour such as bursts of activity, collisions with objects and rapid ventilation (Elliot 1981), aerobic scope and cardiac function can decline (Farrell 1997; Pörtner 2001), susceptibility to disease generally increases (Ellis 1981), oxygen availability decreases, food conversion efficiency decreases (Kinne 1960; Andrews and Stickney 1972; Wurtsbaugh and Davis 1977) and physiological indices of stress such as plasma cortisol levels are elevated (Wendelaar Bonga 1997; Barton 2002). Physiological homeostasis is disturbed through changes in reaction rates and membrane permeability (Hazel 1984), resulting in increased metabolic demand, decreased blood osmolality and serum electrolytes (Houston and Schrapp 1994; Claireaux and Audet 2000) and decreased probability of survival (Elliot 1981). At temperatures below the thermal optimum, fish have a reduced metabolism and aerobic scope and thus an impaired ability to catch prey, escape predators and navigate obstacles. Cold shock (acute decreases in temperature) and very cold temperatures may result in behavioural disturbances such as darting or colliding with objects, loss of dorsoventral orientation or coma (reviewed in Donaldson *et al.* 2008b). Theoretically, overcoming a capture stressor may be more difficult for a fish under thermal stress than for one in an optimal thermal environment. Previous reviews have examined fisheries-related capture in relation to physiological stress and survival (e.g. Arlinghaus *et al.* 2007), but the role of water temperature has not been explicitly reviewed in this context.

The focus of this paper was to conduct a quantitative review examining the role of environmental temperature on the survival and physiological condition of ray-finned fishes (class Actinopterygii) in response to capture and release. Our main objectives were to (i) quantitatively summarize and interpret trends across studies with respect to geographical location, year of study, focal species, objectives, duration and methodological approaches, (ii) quantify the extent to which elevated water temperatures contribute to mortality from fisheries-related capture and release, (iii) determine the role of elevated water temperatures in influencing sublethal parameters, such as physiological stress, and (iv) identify thermal ranges in which thermal effects begin to influence mortality, for species where sufficient data enabled such comparisons. Herein, we quantitatively address each of these objectives to summarize existing knowledge and highlight the novel and integrative approaches currently being explored. Further, we discuss challenges faced in the interpretation of existing research to guide management decisions on fisheries regulations and temperature, using salmon fisheries as a key example.

Methods

Literature search

ISI Web of Knowledge (WK) and Aquatic Sciences and Fisheries Abstracts (ASFA) were used to identify peer-reviewed literature examining the interactions between capture stress and temperature for fishes in the class Actinopterygii. We included papers published from 1965 to December 2009. Keywords were selected using an iterative process, where searches were conducted in both databases and continually revised to maximize the number of relevant articles returned. Once the final sets of keywords were established and the database was assembled, we manually removed irrelevant articles by reading abstracts and full articles where necessary. Articles were excluded if it was not evident from the abstract that the experiment included a capture-type stressor (real or simulated) examined at more than one temperature.

To capture as many articles as possible that examined some form of capture stress under more than one temperature, we used combinations of search terms in two separate searches. To qualify for the first search, papers had to include in their title, abstract or keywords (hereafter collectively referred to as keywords) one term from each of four categories: temperature ('temperature', 'thermal', 'climate change' or 'season'), consequences ('mortality', 'fate', 'survival', 'stress', 'fitness', 'condition', 'behaviour', 'physiology' or 'injury'), capture ('strenuous exercise', 'exhaustive exercise', 'capture and release', 'catch and release', 'by-catch', 'by-catch' 'handling' or 'escape') and taxa ('teleost' or 'fish' or 'Actinopterygii'; WK search only) and must not have any of the exclusion terms ('shellfish', 'crustacean', 'invertebrate', 'mollusc', 'dolphin', 'turtle', 'seabird', 'bird', 'shark', 'whale', 'shrimp', 'prawn', 'nephrop' or 'lobster'). Similarly, the exclusion terms removed all studies examining species other than ray-finned fishes. The second search required papers to identify in their keywords one of the temperature words identified above, as well as 'hooking mortality', 'angling mortality' or 'discard mortality', and to not have any of the exclusion terms listed above. While there is a large body of knowledge studying exercise under different temperatures, we included only those that studied 'strenuous' or 'exhaustive' exercise to represent one of the stressful facets of the capture–release experience (Milligan 1996). All articles resulting from the two searches were put into a database for consideration. Wildcards were used in most search terms (e.g. 'escap*' would capture escapes, escapees, escaped and escape).

This search process was supplemented by a single-pass reading of papers captured in the database search to find relevant studies cited by other authors. Articles examining only culture-related stressors such as transport or confinement were removed. This resulted in a total of 83 peer-reviewed articles (Table 1). One article in our database involved the collective analysis of data from eight previous studies, two of which were included in this review. We did not exclude this article as the majority of included data was not incorporated elsewhere in this review.

Papers that did not mention temperature in their abstract were eliminated, potentially biasing our results towards papers that found an effect of temperature on the lethal or sublethal effects of capture. Those that found no effect of temperature may have been less likely to report that in an abstract than those that detected an effect. We contend that our approach was justified because temperature is widely considered the master factor in the biology of fishes and is acknowledged to influence capture–release mortality in the published reviews on this topic (e.g. Muoneke and Childress 1994; Chopin and Arimoto 1995; Bartholomew and Bohnsack 2005 and Arlinghaus *et al.* 2007). The failure to report the presence or absence of a temperature effect in a capture–release study (if examined) would be a substantial oversight.

Literature review

Articles were queried for publication trends (e.g. continent where research took place, year of publication, journal name), marine or freshwater environment, laboratory or field experiment (or both), holding method [including free-swimming in the field, fish tanks, temporary holding tanks ashore of study area or on a boat, or large artificial (laboratory) ponds], species, capture method or gear type used (or imposed stressor such as exercise or air exposure), temperatures used, temperature context for a particular habitat or species and temperature effects on mortality. In addition, we queried any sublethal indices the authors explicitly chose to examine stress or impairment, including but not limited to physiological metrics such as plasma and muscle metabolites, muscle or tissue constituents

Table 1 All studies included in the current review, listed alphabetically by scientific name of the study species.

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Raat *et al.* (1997)	Effects on growth and survival of retention of rod-caught cyprinids in large keepnets	*Abramis brama, Cyprinus carpio, Leuciscus idus, Rutilus rutilus, Scardinius erythrophthalmus*		*		12–23			
Broadhurst *et al.* (2009)	Mitigating discard mortality from dusky flathead *Platycephalus fuscus* gillnets	*Acanthopagrus australis, Girella tricuspidata, Platycephalus fuscus, Pseudorhombus arsius, Synaptura nigra*	*	*		15–18		*	
Holland-Bartels *et al.* (1989)	Effects of water temperature on the mortality of field-collected fish marked with fluorescent pigment	*Ambloplites rupestris, Lepomis macrochirus, Notropis atherinoides, N. texanus, Perca flavescens, Pomoxis nigromaculatus*	*	*		10–21		*	
Davis and Parker (2004)	Fish size and exposure to air: potential effects on behavioral impairment and mortality rates in discarded sablefish	*Anoplopoma fimbria*		*	*	(10–18)			
Davis *et al.* (2001)	Stress induced by hooking, net towing, elevated sea water temperature and air in sablefish: lack of concordance between mortality and physiological measures of stress	*Anoplopoma fimbria*		*	*	4–16		*	*
Lupes *et al.* (2006)	Capture-related stressors impair immune system function in sablefish	*Anoplopoma fimbria*			*	10–16			
Olla *et al.* (1998)	Temperature magnified postcapture mortality in adult sablefish after simulated trawling	*Anoplopoma fimbria*		*	*	4–20 (18–20)	*	*	*

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Rutecki and Meyers (1992)	Mortality of juvenile sablefish captured by hand-jigging and traps	*Anoplopoma fimbria*	*	*		4–9			
Fritz and Johnson (1987)	Survival of freshwater drums released from Lake Erie commercial shore seines	*Aplodinotus grunniens*	*	*		14–20			
Götz *et al.* (2007)	Comparison of the effects of different linefishing methods on catch composition and capture mortality of South African temperate reef fish	*Boobsoidea inornata, Cheimerius nufar, Chrysoblephus cristiceps, C. laticeps, Pachymetopon aeneum, Spondyliosoma emarginatum*	*	*		Not stated			
Taylor *et al.* (2001)	Catch-and-release mortality rates of common snook in Florida	*Centropomus undecimalis*	*	*		22–30			
James *et al.* (2007)	Catch-and-release mortality of spotted seatrout in Texas: effects of tournaments, seasonality, and anatomical hooking location	*Cynoscion nebulosus*	*	*		16–33	*	*	
Murphy *et al.* (1995)	Mortality of spotted seatrout released from gill-net or hook-and-line gear in Florida	*Cynoscion nebulosus*	*	*		16–31		*	
Alós *et al.* (2009)	Mortality of *Diplodus annularis* and *Lithognathus mormyrus* released by recreational anglers: implications for recreational fisheries management	*Diplodus annularis and Lithognathus mormyrus*	*	*		14–28			
Storck and Newman (1992)	Contribution of tiger muskellunge to the sport fishery of a small, centrarchid-dominated impoundment	*Esox masquinongy x Esox lucius*	*	*		22–28	*	*	

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Milliken *et al.* (2009)	Survival of discarded sublegal Atlantic cod in the northwest Atlantic demersal longline fishery	*Gadus morhua*	*	*		<7 to >14	*	*	
Suuronen *et al.* (2005)	Escape mortality of trawl caught Baltic cod (*Gadus morhua*) – the effect of water temperature, fish size and codend catch	*Gadus morhua*	*	*		3–19	*	*	
Ross and Hokenson (1997)	Short-term mortality of discarded finfish bycatch in the Gulf of Maine fishery for northern shrimp *Pandalus borealis*	*Glyptocephalus cynoglossus, Hippoglossoides platessoides, Pleuronectes americanus, Pollachius virens*	*	*		4–18 (6–19)		*	
Davis and Olla (2001)	Stress and delayed mortality induced in Pacific halibut by exposure to hooking, net towing, elevated seawater temperature and air: implications for management of bycatch	*Hippoglossus stenolepis*		*	*	5–16	*	*	*
Davis and Schreck (2005)	Responses by Pacific halibut to air exposure: lack of correspondence among plasma constituents and mortality	*Hippoglossus stenolepis*		*	*	(10–16)		*	*
Gingerich *et al.* (2007)	Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish	*Lepomis macrochirus*	*	*	*	18–27		*	*

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Hoxmeier and Wahl (2009)	Factors influencing short-term hooking mortality of bluegills and the implications for restrictive harvest regulations	*Lepomis macrochirus*	*	*		18–35	*		
Muoneke (1992)	Seasonal hooking mortality of bluegills caught on natural baits	*Lepomis macrochirus*	*	*		17–30		*	
Cooke and Hogle (2000)	Effects of retention gear on the injury and short-term mortality of adult smallmouth bass	*Micropterus dolomieu*	*	*	*	9–23		*	*
Schreer *et al.* (2001)	Cardiac response to variable forced exercise at different temperatures: an angling simulation for smallmouth bass	*Micropterus dolomieu*			*	12–20	*		*
Bennett *et al.* (1989)	Mortality of tournament-caught largemouth and smallmouth bass in Idaho lakes and reservoirs	*Micropterus dolomieu & Micropterus salmoides*	*	*		7–25		*	
Edwards *et al.* (2004)	Factors related to mortality of black bass caught during small club tournaments in Connecticut	*Micropterus dolomieu & Micropterus salmoides*	*	*		12–31	*	*	
Cooke *et al.* (2004a)	Angling-induced cardiac disturbance of free-swimming largemouth bass (*Micropterus salmoides*) monitored with heart rate telemetry	*Micropterus salmoides*	*		*	13–25			*
Cooke *et al.* (2003)	Cardiovascular responses of largemouth bass to exhaustive exercise and brief air exposure over a range of water temperatures	*Micropterus salmoides*			*	13–25			*

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Gustaveson *et al.* (1991)	Physiological responses of largemouth bass to angling stress	*Micropterus salmoides*	*		*	11–30			*
Meals and Miranda (1994)	Size-related mortality of tournament-caught largemouth bass	*Micropterus salmoides*	*	*		24–33		*	
Neal and Lopez-Clayton (2001)	Mortality of largemouth bass during catch-and-release tournaments in a Puerto Rico reservoir	*Micropterus salmoides*	*	*		23–28	*	*	
Plumb *et al.* (1988)	Survival of caught and released largemouth bass after containment in live wells	*Micropterus salmoides*		*		10–34		*	
Schramm *et al.* (1985)	Survival of tournament-caught largemouth bass in two Florida lakes	*Micropterus salmoides*	*	*		12–30 (11–36)		*	
Schramm *et al.* (1987)	Evaluation of prerelease, postrelease, and total mortality of largemouth bass caught during tournaments in two Florida lakes	*Micropterus salmoides*	*	*		17–30 (25–34)		*	
Suski *et al.* (2006)	The influence of environmental temperature and oxygen concentration on the recovery of largemouth bass from exercise: implications for live-release angling tournaments	*Micropterus salmoides*			*	14–32	*		*
Thompson *et al.* (2008)	Physiology, behavior, and survival of angled and air-exposed largemouth bass	*Micropterus salmoides*	*	*	*	15–21			*

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Weathers and Newman (1997)	Effects of organizational procedures on mortality of largemouth bass during summer tournaments	*Micropterus salmoides*	*	*		27–33			
Wilde and Pope (2008)	A simple model for predicting survival of angler-caught and released largemouth bass	*Micropterus salmoides*		*		7–27			
Wilde *et al.* (2002)	Mortality of black bass captured in three fishing tournaments on Lake Amistad, Texas	*Micropterus salmoides*	*	*		17–28		*	
Bettinger *et al.* (2005)	Hooking mortality and physiological responses of striped bass angled in freshwater and held in live-release tubes	*Morone saxatilis*	*	*	*	8–29	*	*	*
Bettoli and Osborne (1998)	Hooking mortality and behavior of striped bass following catch and release angling	*Morone saxatilis*	*	*	*	12–31 (15–31)		*	
Brick and Cech (2002)	Metabolic responses of juvenile striped bass to exercise and handling stress with various recovery environments	*Morone saxatilis*		*	*	15–25		*	
Dunning *et al.* (1989)	Reducing mortality of striped bass captured in seines and trawls	*Morone saxatilis*	*	*		1–16		*	
Millard *et al.* (2005)	Mortality associated with catch-and-release angling of striped bass in the Hudson River	*Morone saxatilis*	*	*		12–18		*	
Nelson (1998)	Catch-and-release mortality of striped bass in the Roanoke River, North Carolina	*Morone saxatilis*	*	*		16–24	*	*	

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Thompson *et al.* (2007)	Seasonal natural and fishing mortality of striped bass in a southeastern reservoir	*Morone saxatilis*	*	*		Not stated		*	
Tomasso *et al.* (1996)	Physiological responses and mortality of striped bass angled in freshwater	*Morone saxatilis*		*	*	16–32		*	*
Wilde *et al.* (2000)	Bait and temperature effects on striped bass hooking mortality in freshwater	*Morone saxatilis*	*	*	*	6–31		*	
Hunsaker *et al.* (1970)	Hooking mortality of Yellowstone cutthroat trout	*Oncorhynchus clarkii*	*	*		4–17		*	
Marnell and Hunsaker (1970)	Hooking mortality of lure-caught cutthroat trout (*Salmo clarki*) in relation to water temperature, fatigue, and reproductive maturity of released fish	*Oncorhynchus clarkii*	*	*		3–17			
Strange *et al.* (1977)	Corticoid stress responses to handling and temperature in salmonids	*Oncorhynchus clarkii*			*	9–23			
Dotson (1982)	Mortalities in trout caused by gear type and angler-induced stress	*Oncorhynchus mykiss*		*		8–16		*	
Kieffer *et al.* (1994)	Effects of environmental temperature on the metabolic and acid-base responses of rainbow trout to exhaustive exercise	*Oncorhynchus mykiss*			*	5–18			*
Klein (1965)	Mortality of rainbow trout caught on single and treble hooks and released	*Oncorhynchus mykiss*		*		7–14		*	

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Meka and McCormick (2005)	Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature	*Oncorhynchus mykiss*	*		*	7–17			*
Schisler and Bergersen (1996)	Postrelease hooking mortality of rainbow trout caught on scented artificial baits	*Oncorhynchus mykiss*	*	*	*	4–17		*	*
Simpkins *et al.* (2004)	Factors affecting swimming performance of fasted rainbow trout with implications of exhaustive exercise on overwinter mortality	*Oncorhynchus mykiss*		*		4–15		*	
Wydoski *et al.* (1976)	Physiological response to hooking stress in hatchery and wild rainbow trout (*Salmo gairdneri*)	*Oncorhynchus mykiss*	*		*	4–20			*
Davis and Olla (2002)	Mortality of lingcod towed in a net as related to fish length, seawater temperature, and air exposure: a laboratory bycatch study	*Ophiodon elongatus*		*		8–20		*	
Bettoli and Scholten (2006)	Bycatch rates and initial mortality of paddlefish in a commercial gillnet fishery	*Polyodon spathula*	*	*		4–29		*	
Dieterman *et al.* (2000)	Mortality of paddlefish in hoop nets on the Lower Missouri River, Missouri	*Polyodon spathula*	*	*		16–25			

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Dalla Via *et al.* (1989)	Temperature-related responses of intermediary metabolism to forced exercise and recovery in juvenile *Rutilus rutilus* (L.) (Cyprinidae: Teleostei)	*Rutilus rutilus*			*	4–20			*
Pottinger *et al.* (1999)	Plasma cortisol and 17B-oestradiol levels in roach exposed to acute and chronic stress	*Rutilus rutilus*			*	5–16			*
Anderson *et al.* (1998)	Remote monitoring of heart rate as a measure of recovery in angled Atlantic salmon, *Salmo salar* (L.)	*Salmo salar*		*	*	8–20		*	*
Dempson *et al.* (2002)	Effects of catch and release angling on Atlantic salmon, *Salmo salar* L., of the Conne River, Newfoundland	*Salmo salar*	*	*		12–25	*	*	
Galloway and Kieffer (2003)	The effects of an acute temperature change on the metabolic recovery from exhaustive exercise in juvenile Atlantic salmon (*Salmo salar)*	*Salmo salar*			*	6–18			
Thorstad *et al.* (2003)	Effects of hook and release on Atlantic salmon in the River Alta, northern Norway	*Salmo salar*	*	*	*	10–14			*
Wilkie *et al.* (1997)	Influences of temperature upon the postexercise physiology of Atlantic salmon *(Salmo salar)*	*Salmo salar*		*	*	12–23	*	*	
Wilkie *et al.* (1996)	Physiology and survival of wild Atlantic salmon following angling in warm summer waters	*Salmo salar*	*	*	*	6–22	*	*	*

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Jurvelius *et al.* (2000)	Mortality of pike-perch (*Stizostedion lucioperca*), brown trout (*Salmo trutta*) and landlocked salmon (*Salmo salar* m. *sebago*) caught as by-catch in pelagic trawling in a Finnish lake	*Salmo salar, Salmo trutta, Sander lucioperca*	*	*		10–18			
Hyvärinen *et al.* (2004)	Effects of abrupt cold shock on stress responses and recovery in brown trout exhausted by swimming	*Salmo trutta*		*	*	0–14			
Jepsen *et al.* (2008)	The level of predation used as an indicator of tagging/handling effects	*Salmo trutta*		*	*	8–14			*
Turunen *et al.* (1994)	Trawling stress and mortality in undersized (< 40 cm) brown trout (*Salmo trutta* L.)	*Salmo trutta*	*	*	*	10–20	*		*
Nuhfer and Alexander (1992)	Hooking mortality of trophy-sized wild brook trout caught on artificial lures	*Salvelinus fontinalis*	*	*		6–18		*	
Lee and Bergersen (1996)	Influence of thermal and oxygen stratification on lake trout hooking mortality	*Salvelinus namaycush*	*	*		8–13	*	*	
Loftus *et al.* (1988)	An evaluation of lake trout (*Salvelinus namaycush*) hooking mortality in the Upper Great Lakes	*Salvelinus namaycush*	*	*		4–24			

Table 1 (Continued).

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = increased mortality	Warming = increased sublethal impairment
Hoffman *et al.* (1996)	Walleye and sauger mortality associated with live-release tournaments on the Lake Winnebago system, Wisconsin	*Sander canadensis, Sander vitreus*	*	*		24–27		*	
Hyvärinen *et al.* (2008)	Stress and survival of small pike-perch *Sander lucioperca* (L.) after trawling and chilling	*Sander lucioperca*	*	*	*	0–21		*	*
Reeves and Bruesewitz (2007)	Factors influencing the hooking mortality of walleyes caught by recreational anglers on Mille Lacs, Minnesota	*Sander vitreus*	*	*		10–26		*	
Marçalo *et al.* (2008)	Sardine early survival, physical condition and stress after introduction to captivity	*Sardina pilchardus*		*	*	14–26	*	*	
Alós (2008)	Influence of anatomical hooking depth, capture depth, and venting on mortality of painted comber (*Serranus scriba*) released by recreational anglers	*Serranus scriba*	*	*		16–26			
Alós (2009)	Mortality impact of recreational angling techniques and hook types on *Trachynotus ovatus* (Linnaeus, 1758) following catch-and-release	*Trachynotus ovatus*	*	*		17–25			

Symbols indicate studies that included a field component to the research, analysis of mortality, and/or analysis of sublethal impairment metrics are indicated by a symbol in those columns. Temperature range includes the highest and lowest temperatures studied to the nearest °C, (air temperatures in brackets, when measured) but is not suggestive that all temperatures in that range were examined. When no other information is given, means are presented. High temperatures indicate that authors reported the warmest temperature(s) as high for the species studied. Symbols indicate that warmer temperatures were associated with increased mortality, and/or one or more increased sublethal impairment indices.

such as glycogen, adenosine triphosphate (ATP), adenosine diphosphate (ADP), adenosine monophosphate (AMP), ions and hormones, physical injuries caused by gear or handling, behavioural observations, disease and immune impairment, and vulnerability to predation. We collectively termed these 'sublethal impairments'. Within this category, lactate, glucose, cortisol, ATP, ADP, AMP, phosphocreatine (PCr), pyruvate, haematocrit, haemoglobin, glycogen, heart rate, stroke volume, cardiac output, equilibrium loss, ventilation rate, pH, total protein, oxygen consumption, partial pressure of carbon dioxide (PCO_2) and bicarbonate (HCO_3) were classified as measures of stress and exercise physiology. Osmolality, chloride, sodium and potassium concentrations and haematocrit were classified as measures of osmoregulation. Any physical trauma or bodily harm was classified as an index of injury. All other sublethal metrics were classified as 'other'. It is important to note that if studies evaluated injury as a predictor variable but not as a response variable with respect to both capture stressor and temperature, then this was not included in our sublethal impairment category. Variables and classifications used in this review are presented in Appendix 1.

Some variables queried were not always overtly stated in the articles. For example, papers were queried for 'focal sector', which was the target audience or group that results would be applicable to. These included recreational fisheries (sport or leisure fishing), commercial fisheries (fishing for profit), what we termed 'fisheries science' (where the fishery method or sector was not explicitly stated in the title or abstract, but the study relevance to a particular fishery was discussed in the body of the article) and basic science (fundamental biological questions independent of any fisheries sector). Where unavoidable, subjective decisions were made in order to classify papers. Classes were not mutually exclusive for many of the variables (e.g. some articles examined more than one species, gear type or physiological metric), and the result is that percentages of classes within one queried variable do not always sum to 100%.

We queried the papers with regard to several temperature-related questions: what temperatures were studied, were temperatures naturally occurring or manipulated, what was the effect of temperature on stress indices and mortality (e.g. was the effect positive, negative, both or neither) and what was the biological temperature context of the study? For this last question, we looked for authors to place the temperatures examined into context with regard to the focal species and classified them as high, within thermal tolerance ('normal'), low or 'no context given'. All references and summary temperature information are listed by species in Table 1. Articles were queried as to whether increasing temperature had a significant effect on mortality or any sublethal indices quantified and whether this effect was positive (greater survival or lower sublethal impairment parameters), negative or neutral (no effect).

Thermal preference and/or optimal growth temperature data are available on many species; therefore, we attempted to use the existing data in the literature to see if overall patterns in the results presented in this review could illuminate whether final thermal preferendum or optimal temperatures for growth (henceforth 'optimal temperatures') corresponded with optimal temperatures for capture and release. Our chain of reasoning for choosing this parameter was as follows: (i) the final thermal preferendum and the optimum temperature for growth closely approximate one another (Jobling 1981; Kellogg and Gift 1983), (ii) data on optimal temperatures for growth are available for many species, presumably due to their applications in aquaculture, (iii) these parameters may not vary between populations of species that have wide geographical ranges (Beitinger and Fitzpatrick 1979) and (iv) using optimal (growth) or preferred temperatures as a context against which to study capture–release mortality is particularly interesting because within this zone, fish are not thermally stressed given the absence of secondary acute stressors (as opposed to critical temperatures, which are lethal in the short- or long term). This allows us to evaluate whether the optimal thermal window narrows when capture–release stressors are applied.

While it is difficult to compare across studies, because a number of other factors are variable (e.g. air temperature, air exposure, gear types, time in live-wells, water conditioner or aeration, number of monitoring days), we examined the temperature at which mortality began to increase within a given set of circumstances. We examined size classes separately because for many species, there are ontogenetic differences in the optimum temperature for growth, with optimal temperatures decreasing with increasing body size (e.g. Björnsson *et al.* 2001; Imsland *et al.* 2005 and references therein). Presented are the optimal temperatures for species that had more than one mortality study included in this review (Table 2).

Results

Klein (1965) was the earliest peer-reviewed study identified in our database. It was published in *The Progressive Fish-Culturist* (became *North American Journal of Aquaculture* in 1999) and studied hooking mortality in rainbow trout (*Oncorhynchus mykiss*, Salmonidae). Eighty-three studies matched our search criteria, with most of these occurring in the last 20 years (Fig. 1). Studies occurred predominantly in North America (81%) and Europe (17%; Appendix 1), and 76% were focused on freshwater species (Appendix 1). Studies were published in 18 peer-reviewed journals, with more than half of all studies being from one of the American Fisheries Society publications, which include the *North American Journal of Fisheries Management* (45%), and *Transactions of the American Fisheries Society* (14%; Appendix 1). *Fisheries Research* and the *Journal of Fish Biology* were also common publication venues (10 and 8%, respectively).

While the target sector was not always obvious or discrete, the majority focused on the recreational sector (64%), followed by the commercial sector (27%; Appendix 1), with considerable overlap. We classified six studies (7%) as 'fisheries science', because while the title and abstract of the paper were not clearly aimed at a particular fisheries sector, the fisheries applications of the research were discussed in the body of the paper. The remaining four studies (5%) addressed fundamental scientific questions and did not express a direct applied research focus. No studies explicitly examined artisanal or Aboriginal fisheries.

Studies examined 21 families of fishes from nine orders. Perciformes was the most commonly studied order (52%, with 25% of all studies focused on the family Centrarchidae), followed by Salmoniformes (consists of only the family Salmonidae, 28%). Of the 52 species studied, 35 were only examined in one article (Fig. 2). Most papers (88%) investigated a single species. Largemouth bass (*Micropterus salmoides*, Centrarchidae) was the most commonly studied species (18% of total), followed by striped bass (*Morone saxitalis,* Moronidae; 11%), rainbow trout (8%) and Atlantic salmon (*Salmo salar*, Salmonidae; 8%; Fig. 2).

Most studies focused on real or simulated capture stressors (71 studies, 86%; Appendix 1), which include multiple identifiable stressors such as handling, exercise, confinement and air exposure. Other studies focused on specific components of the capture–release experience, which authors identified as strenuous exercise (8%), handling (6%), air exposure (4%) and tagging or sampling (4%). Of the 54 studies examining hook-and-line fishing methods, almost all of these (50 studies, 93%) were focused on the recreational fishing sector. Twelve studies (17% of the 71 capture studies) examined the effects of trawling. Gill nets and purse seines were the capture method in three studies each (4% of the 71 capture studies). An additional three studies employed manual chasing, including two that used this method to simulate angling (Cooke *et al.* 2003; Suski *et al.* 2006) and a third that discussed their results in a recreational fishing context (Wilkie *et al.* 1997). Other fishing methods examined were traps (two studies), beach seines (one study) and hoop nets (one study). No studies compared electrofishing results at multiple temperatures.

Warmer temperatures resulted in higher mortality in 49 of the 70 (70%) papers that quantified survival after capture (84% of all papers quantified mortality). Only one study found lower mortality in warmer water, and in this case, Rutecki and Meyers (1992) speculated that sablefish (*Anoplopoma fimbria*, Anoplopomatidae) mortality was related to disease. Of the 55 studies that were performed in a field setting, most (44 studies, 80% of field studies) used visual assessment to quantify mortality, almost exclusively by utilizing temporary lakeside, streamside or on-board holding tanks. One exception was Loftus *et al.* (1988), who held lake trout (*Salvelinus namaycush*, Salmonidae) by stringers through the lip and tethered them to a buoy. Telemetry was utilized in six studies (11% of field studies), and mark–recapture was used in two studies (4% of field studies). Mortality occurring within <24 h was examined in nine studies (13% of 70 mortality studies) and 1- to 2-day mortality in 15 studies (21%), whereas 23 studies (33%) quantified mortality greater than 2 days but ≤1 week. Twenty-four studies (34%) examined mortality for longer than 1 week.

Thirty-seven articles (45% of all 83 studies) measured sublethal impairments, including physiological indices of stress such as elevations of metabolites or stress hormones in the plasma (57% of 37 sublethal studies) or muscle tissues (16%), cardiac parameters (e.g. heart rate, stroke

Table 2 Comparison of the preferred temperature for growth and/or optimal temperature from the literature with the temperature at which mortality began increasing within a given experiment.

Species	Optimal/Preferred temp (°C)	Temp mortality increased (°C)	Optimal temp references	Capture/temp references
Anaplopoma fimbria	14–22^{a}	14	Sogard and Olla (2001)	Davis *et al.* (2001);
Sablefish	12–15^{b}	no temp effect (10–18 air)		Davis and Parker (2004);
		15		Olla *et al.* (1998);
		no temp effect (4–9)		Rutecki and Meyers (1992);
Cynoscion nebulosis	28^{a}	27	Wohlschlag and Wakeman (1978)	James *et al.* (2007);
Spotted seatrout		28	Kupschus (2003)	Murphy *et al.* (1995);
Gadus morhua	7^{a}	9–14	Björnsson *et al.* (2001);	Milliken *et al.* (2009);
Atlantic cod	13–15^{a}	10	Jobling (1983);	Suuronen *et al.* (2005);
	10–11^{a}		Pörtner *et al.* (2001)	
Hippoglossus stenolepis	10^{a}	16	Björnsson and Tryggvadóttir (1996)	Davis and Olla (2001);
Pacific halibut	3–8^{b}	16 (air temp)	I.P.H.C. (1998)	Davis and Schreck (2005);
Lepomis macrochirus	27–35^{b}	30	Kieffer and Cooke (2009)	Muoneke (1992);
Bluegill		27		Gingerich *et al.* (2007);
		no temp effect (18–35)		Hoxmeier and Wahl (2009);
Micropterus dolomieu	30^{b}	21 (one tournament only)	Barans and Tubb (1973);	Bennett *et al.* (1989);
Smallmouth bass	28.5–32^{b}	22	Kieffer and Cooke (2009)	Cooke and Hogle (2000);
		20–25		Edwards *et al.* (2004);
Micropterus salmoides	27–30^{b}	27	Clugston (1973);	Edwards *et al.* (2004);
Largemouth bass	29–33^{b}	23	Kieffer and Cooke (2009)	Bennett *et al.* (1989)
		28		Meals and Miranda (1994);
		26.5		Neal and Lopez-Clayton (2001);
		31		Plumb *et al.* (1988);
		21		Schramm *et al.* (1985);
		<30		Schramm *et al.* (1987);
		no temp effect (15–21)		Thompson *et al.* (2008);
		no temp effect (27–33)		Weathers and Newman (1997)
		26		Wilde *et al.* (2002);
		no temp effect (7–27)		Wilde and Pope (2008);

Table 2 (Continued).

Species	Optimal/Preferred temp (°C)	Temp mortality increased (°C)	Optimal temp references	Capture/temp references
Morone saxatilis	19–23[b]	28	Coutant (1990);	Bettinger *et al.* (2005);
Striped bass	24[a]	28	Cox and Coutant (1981)	Bettoli and Osborne (1998);
		25 (in buffered water only)		Brick and Cech (2002);
		12–16		Dunning *et al.* (1989);
		16		Millard *et al.* (2005);
		21		Nelson (1998);
		27–29		Thompson *et al.* (2007);
		26		Tomasso *et al.* (1996);
		26		Wilde *et al.* (2000);
Oncorhynchus clarkii	13–15[b]	14–17	McMahon *et al.* (2006)	Hunsaker *et al.* (1970)
Cutthroat trout		no temp effect (3–17)		Marnell and Hunsaker (1970);
Oncorhynchus mykiss	14–15[a]	9–11	Barnabé (1994);	Dotson (1982);
Rainbow trout	11[b]	14	McCauley *et al.* (1977);	Klein (1965);
	13–15[b]	13	McMahon *et al.* (2006)	Schisler and Bergersen (1996);
		15		Simpkins *et al.* (2004);
Polyodon spathula	12–24[b]	18	Crance (1987);	Bettoli and Scholten (2006);
Paddlefish	24–29[b]	no temp effect (16–25)	Paukert and Fisher (2000);	Dieterman *et al.* (2000);
	7–20[c]		Rosen and Hales (1981)	
Salmo salar	15[a]	20	Barnabé (1994);	Anderson *et al.* (1998);
Atlantic salmon	16[a]	14–18	Elliott and Hurley (1997);	Dempson *et al.* (2002);
	14[b]	no temp effect (10–14)	Peterson and Metcalfe (1979)	Thorstad *et al.* (2003);
		20		Wilkie *et al.* (1996, 1997);
		23		
Salmo trutta	12–14[a]	No temp effect (0–14)	Barnabé (1994);	Hyvärinen *et al.* (2004);
Brown trout	16[b]	no temp effect (10–20)	Spigarelli *et al.* (1983)	Turunen *et al.* (1994);
Sander lucioperca	28–30[a,b]	16	Hokanson (1977);	Hyvärinen *et al.* (2008);
Pike-perch	12–30[a]	no temp effect (10–18)	Lehtonen (1996)	Jurvelius *et al.* (2000);
Sander vitreus	21–23[b]	25	Coutant (1977);	Hoffman *et al.* (1996);
Walleye	22–28[a]	18	Hokanson and Koenst (1986)	Reeves and Bruesewitz (2007);

[a] Optimal temperature for growth.
[b] Preferred temperature.
[c] Optimal temperature for feeding.

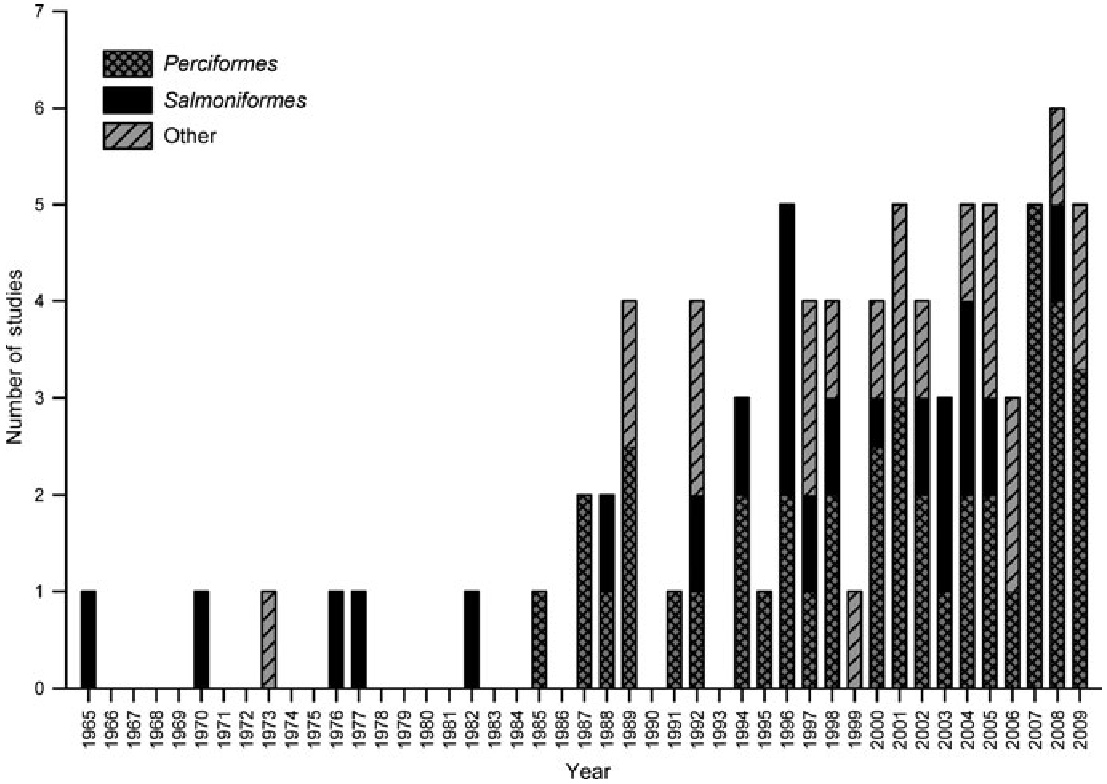

Figure 1 Number of publications by year, with shading indicating taxonomic order.

volume, cardiac output, 11%), behavioural impairment (8%), injury (5%), immune suppression (3%) or vulnerability to predation (3%). Included in these were 23 studies (28% of all studies) that examined both mortality and sublethal indices. Twenty-six of the studies (70% of 37 sublethal studies) demonstrated increasing sublethal impairment with increasing temperature. For studies that presented both survival and sublethal effects, 12 (52% of 23 survival and sublethal studies) showed both increased mortality and a sublethal index of stress or impairment with increasing temperature. Twelve studies compared recovery rates from capture, and warmer temperatures were shown to facilitate or expedite recovery in half of these cases (e.g. Dalla Via *et al.* 1989; Kieffer *et al.* 1994; Wilkie *et al.* 1997; Pottinger *et al.* 1999; Galloway and Kieffer 2003; Hyvärinen *et al.* 2004).

Of the 19 studies that included a temperature deemed high for the focal species, all but one (95% of 19 high temperature studies) detected negative effects of increasing temperature on the survival or impairment indices of captured fish. More than half of all studies (58% of 83 studies) did not put their experimental temperatures into any context with regard to species optima; only two of these reported temperatures that were abnormally high for the associated habitat. We found that for 10 of the 15 most studied species in this review (≥2 mortality studies), mortality began increasing at temperatures within the optimal growth or preferred temperatures from the literature (Table 2).

Discussion

Most studies were published in the recent decade, likely reflecting the increasing interest in science that links temperature and fisheries management because of the growing awareness and concern of climate change (Food and Agriculture Organization of the United Nations 2008). Our finding that the majority of studies occurred in freshwater and in North America, and that half focused on recreational fishing, is likely driven by the popularity of recreational catch-and-release fishing in that continent, where management policies mandate or recommend release of captured fish in several jurisdictions [in Canada, see the Fishery (General)

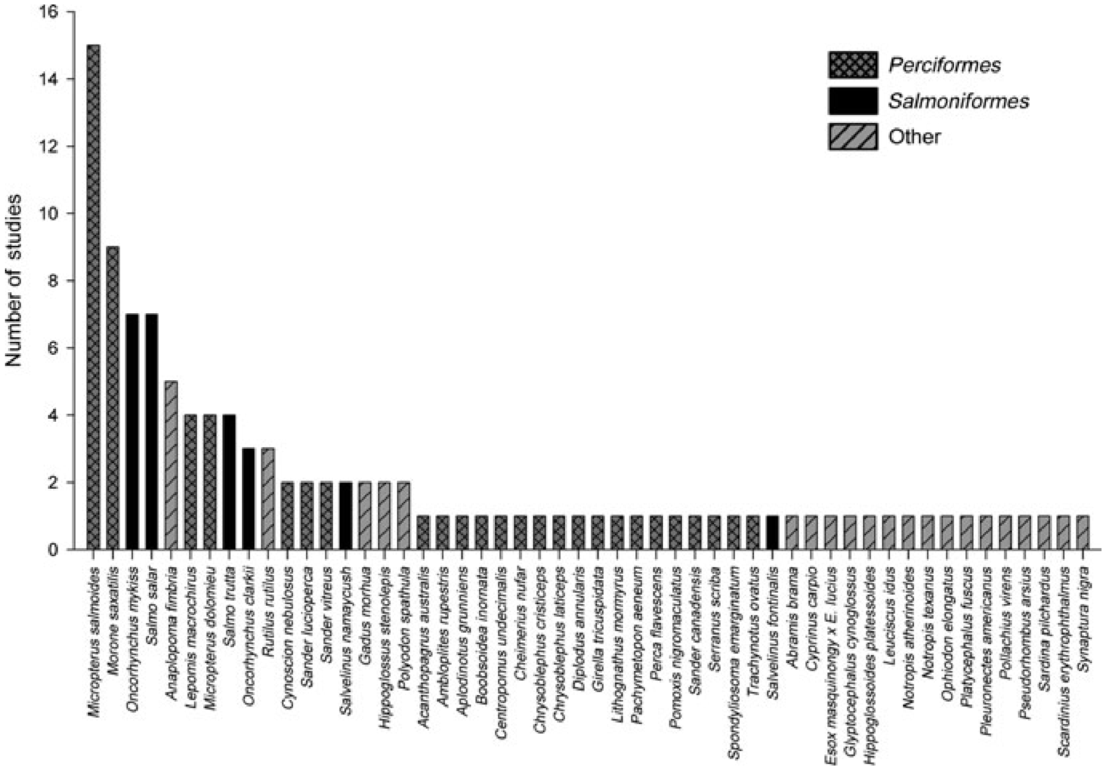

Figure 2 Number of publications by species, with shading indicating taxonomic order.

Regulations – Fisheries Act (1993) or in the United States, see the Magnuson-Stevens Fisheries Conservation and Management Act (2006)]. In contrast, in recent years, some European jurisdictions have banned catch-and-release fishing (described in Arlinghaus 2007) on humane or ethical grounds, and these sorts of policy decisions could be limiting the scientific exploration of capture and release in those regions. The predominance of scientific studies focused on the Centrarchidae and Salmonidae families (53%), a trend consistent with the general pattern of freshwater recreational fisheries in North America. In the United States and Canada, the most common sport fisheries include those for bass (Centrarchidae) and trout (Salmonidae; Fisheries and Oceans Canada 2005, United States Department of the Interior, Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau 2006).

We found that survival study durations from immediate (Meals and Miranda 1994) to up to 2 years (Thompson *et al.* 2007) were well represented in the literature. Several authors suggested that physical injury (Plumb *et al.* 1988; Nelson 1998; Cooke and Hogle 2000), physiological mechanisms such as intercellular acidosis (Wood *et al.* 1983; Milligan and Wood 1986; Kieffer *et al.* 1994) or physiological damage caused by air exposure (Ferguson and Tufts 1992; Davis and Olla 2001; Cooke *et al.* 2002) are leading causes of immediate or short-term (hours) mortality. Although it has been shown that long-term mortality and population-level effects can be linked with immune suppression and subsequent disease development (Wedemeyer and Wood 1974; Wendelaar Bonga 1997), reduced reproductive success of stressed individuals (Schreck *et al.* 2001; Schreck 2010), disrupted gametogenesis because of reallocation of energy during reproductive maturation (Patterson *et al.* 2004), altered courting or mating behaviour or interrupted nest-guarding or other parental care activities (Cooke *et al.* 2002), only a few studies in this review examined factors less directly influencing fitness. For example, Lupes *et al.* (2006) found that sablefish immune function was compromised after the capture stressor (simulated hooking and trawling in laboratory tanks), potentially pre-disposing released fish to disease and delayed mortality, and the response was the same at various water temperatures (up to 16 °C). Other innovative and promising new approaches for studying the effects of thermal and capture stressors used indices of reflex impairment (Davis and Ottmar 2006; Davis 2007, 2010) or vulnerability to predation (e.g. Olla and Davis 1989; Mesa *et al.* 2002). Jepsen *et al.* (2008) found that predation of brown trout (*Salmo trutta*, Salmonidae) by pikeperch (*Sander lucioperca*, Percidae) in laboratory ponds was unaffected by tagging/handling treatments but increased with temperature; however, it is unclear whether this was because of decreased predatory avoidance by the trout or increased predatory effort by the pikeperch in warmer water. Regardless, this experiment investigated an important ecological component of the potential effect of capture and thermal stressors acting together. Our results showed that researchers are beginning to study mortality levels and fitness consequences in a broader context; however, the ultimate population-level effects of the capture and release of fish remains unknown for most species.

Many investigators adopted laboratory-based approaches such that temperatures and other stressors could be precisely manipulated (e.g. Barton and Schreck 1987; Kieffer *et al.* 1994). Although many of the ecological complexities of the real world were not incorporated into this type of research, it can be an important starting point for understanding key relationships between thermal and other stressors. Some studies (Cooke *et al.* 2003; Suski *et al.* 2006) utilized manual chasing to exhaustion in laboratory tanks as a means of simulating the 'playing' and 'landing' components of an angling event under specific thermal conditions and eliciting a stress response similar to that of angling (Milligan 1996). A limitation of this approach is that in addition to physiological stress and exercise, fish sustain injuries from escaping or being released from fishing gears (Chopin and Arimoto 1995; Broadhurst *et al.* 1999; Cooke and Hogle 2000; Davis 2002; Bartholomew and Bohnsack 2005; Arlinghaus *et al.* 2007). Therefore, the results of manual chase studies likely represented a best-case scenario for how captured and released fish responded or survived in relation to specific thermal conditions. For example, while Suski *et al.* (2006) observed no mortality in largemouth bass four hours after simulated angling using manual chasing, Meals and Miranda (1994) reported pre-release mortality in multiple largemouth bass angling tournaments at similar temperatures.

Interpreting mortality rates and stress responses in a laboratory setting is difficult because holding wild fish in pens, tanks or cages can be stressful for some fishes (Billard *et al.* 1981; Barton and Iwama 1991; Conte 2004; Roscoe *et al.* 2010); thus, captivity could contribute to mortality and indices of stress to an unknown degree that is not related directly to a simulated capture–release event. Most field-based experiments also involved holding fish in tanks, albeit temporarily, to assess survival or stress responses. Only six studies in the current review utilized telemetry to assess survival (Lee and Bergersen 1996; Bettoli and Osborne 1998; Thorstad *et al.* 2003; Bettinger *et al.* 2005; Thompson *et al.* 2007, 2008), which allowed for the evaluation of released fish in their natural environment, thus eliminating the effects of captive holding. However, attachment or implantation of transmitters could also contribute to mortality and/or sublethal impairment, and few field studies utilizing telemetry control for tag effects, as monitoring of non-tagged individuals in the field presents substantial logistic challenges. Ideally, researchers would develop and analyse the procedures best suited to their studies (including quantifying detrimental effects) before collecting data (Bridger and Booth 2003). If methodologies are carefully chosen (e.g. using proven surgical techniques and transmitter specifications for the specific study animals and choosing study designs with appropriate control and sham treatments and adequate statistical power; Cooke *et al.* 2011), effects should be minimal and the benefits in terms of data collected are immense (Bridger and Booth 2003; Cooke *et al.* 2004b; Donaldson *et al.* 2008a). Because telemetry is likely one of the best ways to assess both detailed and long-term effects of capture–release on individual survival, and only a small fraction of all studies have adopted this approach, we thus have only a limited understanding of the full extent of the ecological implications of thermal effects on the capture–release of fish.

The primary objectives of this review were to quantify the extent to which elevated water temperatures contributed to mortality from fisheries-related capture and release and determine the role of elevated water temperatures in influencing sublethal parameters, such as physiological stress. The majority of studies found that warmer temperatures had a negative effect on fish condition or survival after release. However, less than one-third of the articles we reviewed integrated mortality and some sublethal index of stress or impairment. There are two very good examples of how such an integrated approach, in the laboratory and field, has helped to elucidate the potential physiological mechanisms responsible for capture-induced mortality. Wilkie *et al.* (1996) examined angling stress by intercepting wild Atlantic salmon in freshwater as they returned to spawn, manually hooking them through the jaw, then playing them to exhaustion. They then sampled fish for blood and white muscle after 0, 2 or 4 h, or observed them for 12 h, to investigate the impacts of fishing in warm summer temperatures (22 °C) versus those at cool fall temperatures (6 °C). They found that summer angling resulted in greater mortality, impaired glycogen resynthesis rates and slowed white muscle lactate elimination and metabolic proton load correction. Olla *et al.* (1998) simulated trawling in adult sablefish, monitoring mortality in laboratory tanks for 60 days and incorporated some basic measures of stress physiology in plasma after the capture simulation. They estimated that the critical post-capture temperature for sablefish that live at 4–6 °C is 12–15 °C and discovered that peak plasma lactate, but not glucose and cortisol, increased with temperature. Plasma lactate and blood pH are both common metrics in capture-and-release experiments because they are a corollary of intracellular acidosis, which may be the reason that fish sometimes die after strenuous exercise (Wood *et al.* 1983). The slower recovery of pH and greater mortality after angling in warm water observed in Wilkie *et al.* (1996) was consistent with that explanation. While Olla *et al.* (1998) did not speculate as to the mechanism underlying the mortality they observed, the integrative nature of their study was beneficial because it analysed the effects of ecologically relevant temperatures for sablefish caught in trawls off the north-west coast of the United States and suggested that in future studies, serum lactate has the potential to be used as a surrogate for mortality. We conclude from the papers we reviewed that the weight of evidence suggests thermal and capture stressors are often additive in nature, such that when experienced together they may be more detrimental to fish than either one experienced alone.

An important, yet surprising, finding in this review was the lack of context given for the temperatures used in more than half of the studies included. Considering that each fish species (and sometimes population) has an optimal temperature (see references in Hart 1952; Beitinger and Fitzpatrick 1979; Johnston and Ball 1997; Beitinger *et al.* 2000; Pörtner 2001, 2002; Farrell *et al.* 2008), it is imperative that the reader understands the context of each temperature for the species and life stage being studied. Indeed, the degree of thermal stress is determined not only by the environmental temperature but also by the species, their genetics and their prior thermal experience (i.e. acclimation; Pörtner 2001). It is not clear whether this has occurred because authors have assumed their target audience was thoroughly knowledgeable of their study organism and thus knew the implications of the experimental temperatures or because they have used the term ‘high’ temperature to suggest that their warmest experimental temperature was not only *relatively* high but also abnormally high for the species or population. Regardless, this widespread lack of temperature context is problematic as it effectively limits the ability of readers to compare or synthesize results across species and habitats. This lack of clarity could lead to confusion over the ramifications of findings in many of these studies. Moreover, because of the large number of papers that fell into this category, it was difficult for us to accurately and succinctly summarize the overall effects of increasing temperatures on capture-and-release experiences in an ecologically meaningful way.

Perhaps the most remarkable finding in our literature review was that temperature-mediated capture–release mortality occurred even within temperatures considered to be optimal or preferred for species with sufficient temperature optimum and preference data to warrant comparison (Table 2). Capture–release mortality of sablefish, spotted seatrout (*Cynoscion nebulosis*, Sciaenidae), Atlantic cod (*Gadus morhua*, Gadidae), bluegill (*Lepomis macrochirus*, Centrarchidae), smallmouth bass (*Micropterus dolomieu*, Centrarchidae), largemouth bass, striped bass, cutthroat trout (*Oncorhynchus clarkii*, Salmonidae), rainbow trout, paddlefish (*Polyodon spathula*, Polyodontidae), pikeperch and walleye (*Sander vitreus,* Percidae) began increasing at temperatures within or below their optimal range (see references in Table 2). We found the exceptions to this trend were Pacific halibut (*Hippoglossus stenolepis*, Pleuronectidae), Atlantic salmon and brown trout. Collectively, these results suggest that temperatures even within preferred or optimal ranges may increase mortality to an unacceptable level for many species, representing a potentially unexpected challenge for managing these fisheries. Generally, optimal and preferred temperature experiments are carried out under idealized conditions. Evidence that a secondary stressor such as capture–release narrows or shifts species' optimal temperature ranges suggests that other secondary stressors, such as poor water quality or disease, may similarly constrict or shift the optimal temperature window. Thus, there is a strong need for researchers to assess the optimal temperature range for a given species under non-idealized conditions.

Management implications

Fisheries managers may refer to scientific capture-and-release literature if they are considering using closures or restrictions to protect threatened species or stocks by reducing the number of harvested individuals. Our finding of a general trend in warm temperatures exacerbating mortality and sublethal impairments suggests that a better understanding of these processes may aid managers in making decisions on fisheries regulations during times of challenging environmental conditions. Dozens of studies examined in the present review recommended avoiding (catch and release) angling or commercial fishing openings (by-catch) when temperatures were relatively high. In some cases, authors recommended a specific temperature threshold above which fishing should be avoided or the resulting increased mortality should be accounted for (e.g. 25 °C for Puerto Rican largemouth bass (Neal and Lopez-Clayton 2001) and 16 °C for Hudson River striped bass (Millard *et al.* 2005)). Other recommendations from the articles in this review include gear or technique recommendations (Klein 1965; Alós 2009), limiting or eliminating air exposure after capture (Cooke *et al.* 2003), improved sorting techniques (Dunning *et al.* 1989) and minimizing handling times (Meka and McCormick 2005).

Nearly one-third (29%) of studies focused on *Oncorhynchus, Salmo and Salvelinus* spp., and although climate warming in the next century may have the most serious effects on cool- and cold-water species such as these, assessing impacts of climate change was rarely stated explicitly as a rationale for the research. For Atlantic salmon, there seems to be sufficient information on the effects of temperature upon capture–release stress and mortality (Wilkie *et al.* 1996, 1997; Anderson *et al.* 1998; Jurvelius *et al.* 2000; Dempson *et al.* 2002; Galloway and Kieffer 2003; Thorstad *et al.* 2003) to aid in the development of specific guidelines for release of captured fish under different thermal conditions. Of the seven articles we uncovered, five found a significant increase in mortality or some sublethal impairment at the highest temperatures (ranging from 14 to 24 °C). Anderson *et al.* (1998) found that after 72 hours, survival declined from 100% at temperatures <16.5 °C to 20% at 20 °C. Wilkie *et al.* (1997) found that 30% of fish released after angling perished at 23 °C, but none perished following release at temperatures <18 °C. Post-angling mortality was 40% in Wilkie *et al.* (1996) at 22 °C. Dempson *et al.* (2002) detected no statistical differences in survival; however, mortality increased from 0% at the coolest temperatures to 12% above 18 °C. Two studies found no effects of increasing temperature (Jurvelius *et al.* 2000; Galloway and Kieffer 2003) up to 18 °C, although Jurvelius *et al.* (2000) found overall high mortality for (landlocked) Atlantic salmon released from trawls when temperatures were 10–18 °C. In summary, temperatures exceeding 20 °C were commonly associated with increased mortality of Atlantic salmon released from fisheries capture, and authors often suggested avoiding catch and release above this temperature.

While some important management guidelines have been implemented based on the results of capture–release science, such as recreational Atlantic salmon fisheries closures when temperatures met or exceeded 22 °C in Newfoundland rivers (Dempson *et al.* 2001), guidelines in North America (state, provincial and federal jurisdictions) often fail to provide useful direction to fishers (Pelletier *et al.* 2007). In their recent review of North American guidelines, Pelletier *et al.* (2007) found that only seven of 49 agencies made recommendations about avoiding catch-and-release fishing in extremely warm water, despite the popularity of angling tournaments in summer months. We reviewed the available online guidelines and discovered that despite the increasing body of knowledge, the proportion of agencies (12 of 61) that warned that post-release mortality might increase in warm water has remained unchanged. The American National Oceanic and Atmospheric Administration's (NOAA) Code of Angling Ethics makes no mention of warm temperatures (NOAA 2010). When agency guidelines do suggest avoiding high temperatures, they almost always fail to state temperature thresholds. For example, in Canada, Atlantic salmon fishing is governed by the federal government (Fisheries and Oceans Canada), whose 'Angler's Guide' recommends that catch and release of Atlantic salmon should cease during 'extreme environmental conditions (low water levels and high water temperatures)' (Fisheries and Oceans Canada 2010). The Atlantic Salmon Federation guide on live-release also recommends avoiding fishing in 'high temperatures', but also neglects to state how high is too high (Atlantic Salmon Federation 2010). We contend that a specific temperature threshold is imperative to angler compliance, simply because vague recommendations fail to inform anglers, even when they have intentions of using best practices. However, we recognize that such recommendations are challenging given the general paucity of data identified here and our finding that even within species-specific thermal preferenda, capture–release mortality may increase.

Conclusion and future directions

Collectively, the studies we reviewed found that temperature stress often contributed significantly to the levels of impairment and mortality of fish released after capture. Very few studies examined the effects of high temperatures that are ecologically meaningful in terms of current peak temperature events in a given habitat or future projections of climate change, as was evident by the lack of supporting context for the experimental temperatures. Our finding that warm temperatures can increase mortality within species-specific optimal temperature ranges demonstrates the importance of evaluating temperature effects in context to improve capture-and-release research and regulations. Future research should use standardized methodologies to determine how thermal stress interacts with capture stressors. Improved communication of the ecological context and management implications of research would allow the incorporation of more research findings into the regulatory planning process. Ideally, authors will explicitly compare their results with optimal or preferred temperature ranges for the study species. Because global climate change may result in the capture and release of fish in warming environments, we must attempt to gain greater insight into the synergistic effects of thermal and capture stressors for species that are frequently released from capture. This is especially urgent for species or populations whose numbers are threatened with precipitous declines or extinction. For example, Pacific salmon (anadromous *Oncorhynchus* spp.) are similarly vulnerable to capture–release and warm temperatures as Atlantic salmon, making them excellent candidates for this type of research. To our knowledge, there is a complete lack of peer-reviewed studies combining thermal and capture–release stressors on adult anadromous Pacific salmonids. This paucity exists despite the fact that some populations of Pacific salmon are threatened or endangered and living in environments already affected by climate change (e.g. sockeye (*O. nerka*, Salmonidae) in Washington and British Columbia, and coho (*O. kisutch*, Salmonidae) from California to British Columbia (Brown *et al.* 1994; Gustafson *et al.* 2007)). Further, these species are still highly sought after by fisheries, and climate change projections suggest continuing future warming (Morrison *et al.* 2002; Ferrari *et al.* 2007), making this type of research warranted for these species.

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Appendix 1

Summary of variables queried of each study, response classes and the number of studies that fell into each class.

Variable	Class	Studies
Order	Perciformes	43
	Salmoniformes	23
	Scorpaeniformes	7
	Cypriniformes	4
	Pleuronectiformes	4
	Gadiformes	3
	Acipenseriformes	2
	Clupeiformes	1
	Esociformes	1
Journal	North American Journal of Fisheries Management	37
	Transactions of the American Fisheries Society	12
	Journal of Fish Biology	7
	Fisheries Research	8
	Fisheries Management and Ecology	4
	Progressive Fish-Culturist (NAJA)	2
	Canadian Journal of Fisheries and Aquatic Sciences	2
	Journal of Applied Ichthyology	1
	African Journal of Marine Science	1
	California Fish and Game	1
	Diseases of Aquatic Organisms	1
	Hydrobiologia	1
	ICES Journal of Marine Science	1
	Journal of Experimental Biology	1
	Journal of Freshwater Ecology	1
	Physiological Zoology	1
	Physiological and Biochemical Zoology	1
	Texas Journal of Science	1

Appendix 1 (Continued).

Variable	Class	Studies
Continent	North America	67
	Europe	14
	Africa	1
	Australia	1
Environment	Freshwater	62
	Marine	18
	Both	1
	Estuary	2
Experiment	Laboratory	28
	Field	51
	Both	4
Stressor	Capture	71
	Exercise	7
	Handling	5
	Air	3
	Tagging/Sampling	3
Sector	Recreational	51
	Commercial	20
	Fisheries Science	6
	Basic Science	4
	Recreational and Commercial	2
Fishing Gear Type	Hook/line (includes longline)	54
	Trawl	12
	Gill net	3
	Manual (Hand) Chase	3
	Purse seine	3
	Traps	2
	Beach seine	1
	Hoop net	1
Holding Method	Brief Holding (lake or streamside, boat)	39
	Holding tanks	30
	Free-swimming – field	15
	Large experimental pond	4
Mortality Assessment	Visual	64
	Telemetry	6
	Mark/Recapture	2
Sublethal Impairment Measures	Stress & Exercise physiology	29
	Osmoregulatory physiology	12
	Behaviour	3
	Immune Impairment	2
	Injury	1
	Predation vulnerability	1
	Reproductive physiology	1

Appendix 1 (Continued).

Variable	Class	Studies
Species Temperature Context	None	48
	High	19
	Moderate/Optimal/Normal	12
	Low	2

Note that classes are not mutually exclusive, i.e. one article may fall into more than one class per variable. See Methods section, for more details on classifications.