Determinants of Hooking Mortality in Freshwater Recreational Fisheries: A Quantitative Meta-Analysis

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Abstract.—In recreational fisheries, catch and release is widespread and practiced under the assumption that released fish survive the capture event unharmed. To improve understanding about the lethal impacts of catch-and-release recreational angling, a quantitative meta-analysis of the literature on hooking mortality and its determinants was conducted focusing on freshwater fishes. Studies were initially selected based on the occurrence of the study species in European recreational fisheries. Because original studies from European freshwater or diadromous fish species were rare, studies from the same genus as native European species were also included in the meta-analysis. Mean hooking mortality \pm SE across all species was 15.9 \pm 1.3% (n = 252 hooking mortality estimates in n = 107 studies), with a median of 7.8% and a range from 0% to 88.5%. The distribution of hooking mortality estimates was highly skewed towards low values; about 60% of all hooking mortality values were below 10%. Average hooking mortality varied between fish families and was highest for Percidae (mean \pm SE, 19.9 \pm 5.3%) followed by Salmonidae (15.9 \pm 1.4%), Esocidae (14.9 \pm 7.0%), and Cyprinidae $(5.7 \pm 1.6\%)$. Hooking mortality was positively related to water temperature and was significantly higher for natural baits and barbed hooks than for artificial baits and barbless hooks. Size of fish and type of hook were unrelated to the level of hooking mortality. To minimize hooking mortality on European fish species, we recommend the use of barbless hooks and artificial baits and we suggest avoiding catch and release of fish during high water temperatures. Further research on the impacts of catch and release on a number of European fishes is recommended because of the limited coverage of species-specific information in the contemporary literature.

Introduction

Globally, the majority of fish captured by recreational anglers are released (Cooke and Cowx 2004; Bartholomew and Bohnsack 2005), either voluntarily (Arlinghaus 2007) or mandatorily as a byproduct of harvest regulations (Polican-

sky 2002; Arlinghaus et al. 2007b). Most catchand-release regulations assume that released fish will survive the event unharmed (Wydoski 1977; Policansky 2002). However, not all fish that are released survive (Muoneke and Childress 1994), and even low hooking mortality levels might result in high levels of cumulative fishing mortality impacting fish populations

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(Bartholomew and Bohnsack 2005; Coggins et al. 2007). Therefore, fisheries managers and other stakeholders are interested in determining the actual hooking mortality of popular fish species, as well as the intrinsic, environmental, and fishing-related factors that increase the probability of postrelease survival.

A great deal of catch-and-release studies have been conducted since the first paper on catch-and-release mortality appeared in the 1930s by Westerman (1932) (reviewed in Wydoski 1977; Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007b). However, a number of open questions about the impact of catch-and-release angling still remain (see Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007b). Moreover, from the pool of species that are targeted and released by anglers, only a minor fraction has been analyzed in depth with respect to their reaction to a catch-and-release event (Cooke and Suski 2005), and only very recently have European researchers started to engage in dedicated catch-and-release research (Arlinghaus et al. 2007b).

In the first comprehensive review on hooking mortality, Muoneke and Childress (1994) analyzed 76 studies. They reported 132 hooking mortality estimates from 32 fish taxa, but they were focused exclusively on fish species of recreational importance to the United States of America (North American salmonids, percids [e.g., walleye Sander vitreus] and centrachides [e.g., black bass Micropterus spp. and bluegill Lepomis macrochirus]). Bartholomew and Bohnsack (2005) provided an update of the early work by Muoneke and Childress (1994). They reviewed 53 studies and reported a total of 274 hooking mortality estimates for 48 fish taxa, including several marine fish species (e.g., Scombridae Thunnus spp.). Bartholomew and Bohnsack (2005) were the first to quantitatively analyze the determinants of hooking mortality in fish in a rigorous meta-analysis framework. However, because the likelihood of death is likely to be family-specific or even species-specific (Cooke and Suski 2005), it is uncertain whether generic hooking mortality analyses that lump species from different environments (e.g., saltwater and freshwater) into one data set can provide generalizable insights. Moreover, although some speciesspecific meta-analyses have been conducted for salmonid species (Taylor and White 1992; Schill and Scarpella 1997), no study has systematically compiled the available information on hooking mortality of central European freshwater or diadromous fish species (i.e., those species of importance for recreational fisheries that occur in mainland Europe).

The objective of our study was to conduct a meta-analysis of hooking mortality studies and their determinants focusing on fish genera of importance in European recreational freshwater fisheries. In the present paper, we analyze the variability of hooking mortality estimates for different fish families and conduct a quantitative analysis with respect to five paramount determinants of hooking mortality for which sufficient information was available in the peerreviewed literature. We compared our results to those generated by Bartholomew and Bohnsack (2005) using a different data set and a different inference statistical approach. Our goal was to test whether insights on the determinants of hooking mortality are generalizable across species families and groups focusing on genera of importance to European freshwater recreational fisheries.

Methods

A uniform literature search for peer-reviewed studies related to catch and release of species of importance in European recreational fisheries was conducted. To ensure that the literature base was as complete as possible, different search approaches were used. First, the references of previous reviews of hooking mortality in recreational angling (Wydoski 1977; Taylor and White 1992; Muoneke and Childress 1994; Schill and Scarpella 1997; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007b) were consulted for an initial compilation of studies. In addition, electronic search services of scientific literature were used. Specifically, we used ASFA (Aquatic Sciences and Fisheries Abstracts), Web of Science, ScienceDirect, Blackwell Synergy, American Fisheries Society, and SpringerLink. Furthermore, we used Google Scholar (www.scholar.google.com). We operated with keywords alone (e.g., "hook" and "hooking") and with keyword strings such as "catch and release," "catch-and-release," "recreational fish*", "hooking mortality," "hook type," "artificial bait," "angling," "angler," "sport fishing," "air exposure," "handling," "sublethal effect*", and "sub-lethal effect*." During the literature research, we mainly focused on peer-reviewed articles and neglected gray literature from North America because of their lack of accessibility in Europe. The detailed literature search was conducted between December 15 and 31, 2007 by the first author of the present paper.

At the onset of our study, we were aware that the total number of European catch-andrelease studies would probably be too low to allow a rigorous meta-analysis. Therefore, we compiled a data set of studies realized with species within genera of importance in European recreational fisheries (e.g., Sander spp., Oncorhynchus spp., and Esox spp.), focusing on freshwater and diadromous fish species. We decided to compile all catch-and-release studies conducted for species of importance to European recreational fisheries irrespective of the species actually being native to Europe or not, under the assumption that species from the same genus would exhibit similar reactions to the catch-and-release event. For example, studies about the hooking mortality of walleye and sauger Sander canadensis were considered relevant for the congeneric zander S. lucioperca. Furthermore, we embraced studies on rainbow trout Oncorhynchus mykiss and cutthroat trout O. clarkii as relevant species in the analysis because they were introduced to Europe (Crawford and Muir 2008) and are nowadays legally identified as native in some countries such as Germany (Kottelat and Freyhof 2007). Because of the importance of Oncorhychus spp. in European recreational fisheries, we also included hooking mortality studies of other non-European species from this genus (e.g., Chinook salmon O. tshawytscha and coho salmon O. kisutch) into the analysis.

From each identified hooking mortality study, key data were extracted, such as species covered, hooking morality estimate(s), environment (e.g., water temperature), fish length, fishing-related variables (e.g., gear choice), study design, and the country where the study was conducted (Table 1). We decided to include all identified literature, even in the case of weak experimental design, (e.g., lack of appropri-

ate controls) to increase sample size. Reported survival rates per study were converted into percent mortality. Furthermore, reported initial and/or delay hooking mortality were converted into total mortality, as described by Wilde (1998). We extracted the most important determinants of hooking mortality from each study based on earlier syntheses by Wydoski (1977), Muoneke and Childress (1994), and Bartholomew and Bohnsack (2005). We assumed that the most important determinants of hooking mortality reported in these studies would also apply to European species and/or to species of genera of importance for European recreational fisheries. The final set of potential determinants of hooking mortality comprised water temperature (e.g., Lee and Bergersen 1996; Wilde et al. 2000; Graeb et al. 2005), length of fish (e.g., Dedual 1996), hook type (single versus treble, e.g., DuBois and Dubielzig 2004), existence of a barb on the hook(s) (e.g., DuBois and Dubielzig 2004; DuBois and Kuklinski 2004), and type of bait coded as organic (i.e., natural) versus artificial (e.g., Arlinghaus et al. 2008). Constraints on salient alternative determinants of survivability were caused by too few or no data on further potential factors of hooking mortality (e.g., anatomical hook location, hook size, and capture depth).

Water temperatures were reported with varying precision in the original studies. For example, some authors reported the exact water temperature while others only provided a temperature range over the entire study period. For our analysis, we used the temperature reported in the study or calculated the midpoint within the reported water temperature range. Similarly, when studies reported a range of fish lengths (in millimeters), we used the midpoint fish length for our analysis. Because fish length was not reported in a uniform manner across the studies, total fish length was calculated according conversion equations given by Froese and Pauly (2008). The total length of a fish was categorized into either legal or nonlegal (undersized). To categorize the species into legal categories, a size threshold according to the most common minimum-size limits reported in the various German fisheries bylaws was determined (Table 2). We used the German minimum-size limits because they usually encompass the smallest standards applied to European fish species due

Table 1.—List of hooking mortality studies (n = 107) used in the meta-analysis. Data on mortality, water temperature, fish length, bait type, hook type, study design, sample size (N), and country in each study are presented. Bait type was categorized as artificial (artificial bait) and natural (natural bait). Single hooks were abbreviated as "single" and treble hooks as "treble." Barbed hooks are indicated with "+" and barbless hooks with "-". The column study design describes the method and environment in which the study was conducted. Sample size refers to the stated mortality estimation in the corresponding row, and an additional tick mark "" labels the inclusion of a control group. The country column depicts the location of the hooking mortality study. References marked with asterisks were not seen but secondarily cited: * cited by Muoneke and Childress (1994), ** cited by Wydoski (1977), and *** cited by Dextrase and Ball (1991). Data used for comparisons in Table 4 are marked with ‡0 (undersized fish), ‡1 (legal-sized fish), §0 (artificial bait), §1 (natural bait), #0 (single hook), #1 (treble hook), \$0 (barbed hook) and \$1 (barbless hook). Temp. = temperature; obs. = observation; sim. = simulated.; telem.= telemetry; nat. = natural

Milne and Ball (1956) Consultants (1989)* Gjernes et al. (1993) Vincent-Lang et al. Parker et al. (1959) Butler and Loeffel Falk and Gillman Natural Research (1975)*/** Schill (1996) (1993)(1972)Washington Location Canada Oregon Alaska Canada Canada Alaska Alaska Idaho 152 107 × 282 209 30 156 3 282 65 1,032 384 Z 81 Environment Holding pen Raceway Raceway Raceway ive box **Tank Tank** Fank Study design Mark-recapture Mark-recapture Mark-recapture Mark-recapture Mark-recapture Mark-recapture 51-d obs. 51-d obs. 51-d obs. 61-d obs. 51-d obs. 51-d obs. Method 2-d obs. 2-d obs. 2-d obs. 6-h obs. 6-h obs. 6-h obs. 2-d obs. 2-d obs. 2-d obs. 5-h obs. Single+#0, \$0 [reble+#1, 50 [reble+#1, 50 Hook type Single-#0,\$1 Single-#0, \$1 [reb]e+#1,50 reble-#1,\$1 Single#0 Single¹⁰ Single²⁰ Single*0 Single** reble*1 Single** reble#1 Single** Artificial⁸⁰ Artificial^{§0} Artificial⁹⁰ Artificial^{§0} Artificial^{§0} Artificial⁸⁰ Artificial⁸⁰ Artificial^{§0} Artificial^{§0} \rtificia | §0 Artificial⁵⁰ Artificial^{§0} Artificial^{§0} Artificial^{§0} Artificial^{§0} \rtificial^{§0} Bait type Vatural^{§1} Vatural^{§1} Vatural^{§1} Natural^{§1} Vatural^{§1} Vatural^{§1} Natural^{§1} Vatural^{§1} Natural^{§1} 10.0-13.0 203-406 25-309 125-309 32-254 75-405 175-405 381-610 25-309 32-254 32-254 203-406 Length (mm) 245^{t0} >1000 $245^{‡0}$ 11.0-13.5 11.0-13.5 10.0 - 14.00.0-14.0 10.0 - 14.010.0-13.0 0.0-14.0 3.0-15.0 15-19 9.5-13.5 15-19 15 - 19Temp (°C) 7.5 12.7 12.7 Mortality 14.0 16.0 42.0 33.0 1.9 47.4 74.3 0.9 12.6 8.6 Thmallus articus Oncorhynchus Arctic grayling Arctic grayling Rainbow trout Coho salmon Coho salmon Coho salmon Coho salmon Coho salmon Salmonidae Coho salmon O. mukiss kisutch Species

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Ve	Mortality	Temp.	Length	(6)		Study design	žu.			*
Species	(%)	(Ĉ)	(mm)	Bait type	Hook type	Method	Environment	Z	Location	Reference
Rainbow trout	0:0	17-20	175-325#1	Artificial ^{§0}	Single_#0,\$1	26-d obs.	Live box	150~	California	Jenkins (2003)
7)	8.7	17-20	$175-325^{\dagger 1}$	Artificial ^{§0}	Single-#0.51	26-d obs.	Holding pen	150		
	2.0	17-20	$175-325^{41}$	Artificial ^{§0}	Single-#0,51	26-d obs.	Holding pen	150		
40	0.0	17–20	175-325#	Artificial ^{§0}	Single_#0,51	26-d obs.	Holding pen	150		
pote	2.0	17-20	$175-325^{‡1}$	Artificial ⁵⁰	Treble-#1, \$1	26-d obs.	Holding pen	150		
	0.7	10-16		Artificial ^{§0}	Single**	e0-d obs.	Holding pen	300		
**	4.7	10.5-14.5		Artificial ^{§0}	Single-#0.51	21-d obs.	Stream section	150		
	0.7	10.5-14.5		Artificial ^{§0}	Single-#0,51	21-d obs.	Stream section	150		
	3.3	10.5-14.5		Artificial ^{§0}	Single-#0,51	21-d obs.	Stream section	150	2	
Rainbow trout	2.0			Artificial ^{§0}	Single+-#0	Blood sampling		415	Alaska	Meka and
				2 "						McCormick (2005)
Rainbow trout	3.9		186-440 ^{±1}	Artificial ^{§0}	Single*0	21-d obs.	Holding pen	457	Colorado	Schisler and
200	21.6	4.0-17.0	$186 - 440^{\sharp 1}$	Artificial ⁹⁰	Single**	21-d obs.	Holding pen	505		Bergersen (1996)
	32.1		$186-440^{\ddagger1}$	Artificial ^{§0}	Single**	21-d obs.	Holding pen	511		
Rainbow trout	3.5		97-37840	Artificial ⁵⁰	Treble+*1, \$0	2-d obs.	Holding pen	255	Wisconsin	DuBois and
	4.8		$97 - 378^{40}$	Artificial ^{§0}	Treble-#1,51	2-d obs.	Holding pen	167		Dubielzig (2004)
	3.1		97-37840	Artificial ⁹⁰	Single+*0,50	2-d obs.	Holding pen	160		
	1.8		97-378	Artificial ^{§0}	Single_#0,51	2-d obs.	Holding pen	114		
Rainbow trout	72.0	15.0	y.	Sim. angling)	12-h obs.	Tank	1	Canada	Ferguson and Tufts
	38.0	15.0		Sim. angling		12-h obs.	Tank	>	38	(1992)
	12.0	15.0		Sim. angling		12-h obs.	Tank	8		
Rainbow trout	3.6	4.0-7.0	$782 - 940^{11}$	1		7-month telem.	River	226	Canada	Nelson et al. (2005)
Rainbow trout	39.5	9.4 - 16.1	W	Natural ^{§1}	Single*0	3-d obs.	Holding pen	38	Washington	Pauley and Thomas
	46.5	9.4 - 16.1		Natural ^{§1}	Single**	3-d obs.	Holding pen	43		(1993)
	58.1	9.4–16.1		Natural ^{§1}	Single**	3-d obs.	Holding pen	43		
	40.7	9.4 - 16.1		$Natural^{\S 1}$	Single#0	3-d obs.	Holding pen	27		
	10.5	9.4 - 16.1		Artificial ⁵⁰	Treble*1	3-dobs.	Holding pen	38		tu:
	23.8	9.4 - 16.1		Artificial ^{§0}	Treble*"	3-d obs.	Holding pen	42		
ste.	15.9	9.4 - 16.1	3	Artificial ^{§0}	Single**	3-d obs.	Holding pen	4		
Rainbow trout	15.3	16.8	288‡1		Single**	1-d obs.	Holding pen	25	New Zealand	New Zealand Dedual (1996)
	14.0	16.8	588‡1	v	Single**	1-d obs.	Holding pen	20		2
	7.8	16.8	58841		Single**	1-d obs.	Holding pen	51		
	2.2	16.8	588‡1		Single**	1-d obs.	Holding pen	46		

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	Mortality	Temp.	Length			Study design	ign			
Species	(%)		(mm)	Bait type	Hook type	Method	Environment	Z	Location	Reference
Rainbow trout	2.9	8.9	22410	Sim. angling	200	30-d obs.	Raceway	105	Montana	Dotson (1982)
	0.0	8.4	24940	Sim. angling		30-d obs.	Raceway	105		
	5.7	15.0	173^{10}	Sim. angling	- ngow	30-d obs.	Raceway	105		
	4.8	15.0	23940	Sim. angling		30-d obs.	Raceway	105		
	8.6	16.7	236^{40}	Sim. angling		30-d obs.	Raceway	105		
	2.9	11.1	249 ^{‡0}	Sim. angling		30-d obs.	Raceway	105		
Rainbow trout	87.0	6.0-10.0	200^{40}	Artificial ⁵⁰		10-d obs.	Tank	16	Michigan	Bouck and Ball (1966)
Rainbow trout	8.0	19.0-20.0		Artificial ¹⁸⁰		35-d obs.	Raceway	101	Colorado	Horak and Klein
										(1967)
Rainbow trout	23.0	4.0		Natural ^{§1}	Single+*0,50				Colorado	Klein (1974)**
Rainbow trout	10.0		249 ^{‡0}	Artificial ^{§0}		2-d obs.	Live box	164	Colorado	Klein (1966)
	11.0		249^{+0}	Artificial ^{§0}	*	2-d obs.	Live box	80		
	16.0		249 ^{‡0}	Artificial ⁹⁰		2-d obs.	Live box	32		
	22.0		249 ^{‡0}	Artificial ⁵⁰	. AP	2-d obs.	Live box	833		
Rainbow trout	39.0	12.0-13.0		Natural ^{§1}	8	10-d obs.	Holding pen	18	South Carolina	South Carolina Barwick (1985)
	5.0	12.0-13.0		Artificial ^{§0}		10-d obs.	Holding pen	20		
Rainbow trout	88.5		145^{20}	Natural ^{§1}		4-month obs.	Tank	200	Wisconsin	Mason and Hunt
	34.5		145^{+0}	Natural ^{§1}		4-month obs.	Tank	200		(1967)
Rainbow trout	6.1	7.0-14.0	$173 - 302^{40}$	Artificial ⁵⁰	Single**	3-d obs.	Raceway	505	Colorado	Klein (1965)
	3.4	7.0-14.0	173-302 ^{t0}	Artificial ^{§0}	Treble*1	3-d obs.	Raceway	495		
Rainbow trout	5.7	15.0-17.0	$193-344^{‡0}$	Artificial ⁵⁰	Treble*1	2-d obs.	Holding pen	332	Canada	Stringer (1967)
	36.0	15.0-17.0	193-344 ^{t0}	Natural ^{§1}	Single**	2-d obs.	Holding pen	239		
Rainbow trout	20.0	12.0-17.0	471^{11}	Artificial ⁹⁰	Single+#0.50	2-d obs.	Holding pen	53	Canada	Facchin (1983)
Rainbow trout	5.2		79-27240	Artificial ^{§0}	Single, treble	1-d obs.	Live crate	346	Michigan	Shetter and Allison
										(1958)
Rainbow trout	11.3		102-20140	Artificial ^{§0}	Single"	1-d obs.	Live crate	8	Michigan	Shetter and Allison
	35.4		102-201 ^{‡0}	Natural ^{§1}	Single**	1-d obs.	Live crate	2		(1955)
Rainbow trout	3.3	10.0-14.4		Natural ^{§1}	Single+#0,50			61	New Mexico	Thompson (1946)**
N.S.	5.9			Artificial ^{§0}	Single+160,50			21		79
	5.0			Artificial ⁵⁰	Single-*0, \$1			3		
Rainbow trout	3.9	15.5		Artificial ^{§0}	Single-*0.51			129	Washington	Wydoski (1970)**
Rainbow trout	1.2		. 352‡1	Artificial ^{§0}	Single+, -*	***		999	Alaska	Meka (2004)
Rainbow trout	3.0	15.0-16.0	15.0-16.0 212-33411	Sim. angling Single+#0.50	Single+#0.50	30-d recovery	Tank		Texas	Pope et al. (2007)

Table 1.—Continued.

	Mortality	Temp.	Length			Study design	ESU.	11	1	ı
Species	(%)	(C)	(mm)	Bait type	Hook type	Method	Environment	Z	Location	Reference
Cutthroat trout	2.9	2.7-9.4	274-442#1	Artificial ^{§0}	Treble*1	30-d obs.	Live box	102	Wyoming	Marnell and Hunsaker
O. clarkii	6.5		$274 - 442^{11}$	Artificial ^{§0}	Treble*1	30-d obs.	Live box	2007		(1970)
	4.0	14.4–16.7	$274 - 442^{11}$	Artificial ^{§0}	Treble*1	30-d obs.	Live box	20		
Cutthroat trout	0.3	11.1	211^{40}	Artificial ⁵⁰	Single, treble+,-	30-d obs.	Raceway	315	Montana	Dotson (1982)
Cutthroat trout	0.3	11.0-17.0	391#			Carcass obs.	River		Wyoming	Schill et al. (1986)
Cutthroat trout	0.7	10.0		Artificial ^{§0}	Treble+#1,50	=			Wyoming	Benson and Bulkle
	21.3	17.0		Artificial ^{\$0}	Treble+*1					(1963)
Cutthroat trout	2.4	7.0		Artificial ⁹⁰	Treble+#1, \$0			503	Idaho	T. C. Bjornn (personal
	4.0	7.0		Artificial ^{§0}	Single+*0, \$0			256		communication to
	0.8	7.0		Artificial ^{§0}	Single-#0, \$1			264	20	R. S. Wydoski)**
	1.2	7.0		Artificial ^{§0}				166	9	
Cutthroat trout	4.0		250-42411	Artificial ^{§0}	Single+#0,50	10-d obs.	Live box	75	Wyoming	Hunsaker et al. (1970)
	3.3		250-424#1	Artificial ^{§0}	Single-#0,51	10-d obs.	Live box	209		e.
	2.7	4.5-16.9	$250-424^{11}$	Artificial ⁵⁰	Treble+#1,50	10-d obs.	Live box	113		
	6.0	4.5-16.9	250-424	Artificial ^{§0}	Treble-#1, \$1	10-d obs.	Live box	100		
	8.2	4.5-16.9	250-424 ^{‡1}	Artificial,	Single**	10-d obs.	Live box	61	r	
				natural	•		2			
	73.0	4.5 - 16.9	250-424#	Artificial,	Single#0	10-d obs.	Live box	100		
				natural		V				
Cutthroat trout	0.0	5.5-11.0		Artificial ⁹⁰	Single-#0,\$1	4-d obs.	Live box	110	California	Titus and Vanicek
	2.1	5.5-11.0		Artificial ⁵⁰	Treble-#1, \$1	4-d obs.	Live box	92		(1988)
	2.6	5.5-11.0		Artificial ^{§0}	Treble+#1,50	4-d obs.	Live box	7		
	59.1	6.0-21.0		Artificial ^{§0}	Single-#0, \$1	4-d obs.	Live box	99		
	35.3	6.0-21.0		Artificial ⁵⁰	Treble-#1, \$1	4-d obs.	Live box	21		
	48.1	6.0-21.0	235-491 ^{‡1}	Artificial ^{§0}	Treble+#1,50	4-d obs.	Live box	22		
	0.0	10.5-15.5	216-537#1	Artificial ^{§0}	Single-#0, \$1	4-d obs.	Live box	56		
	3.5	10.5-15.5	216-537#1	Artificial ^{§0}	Treble-"1, \$1	4-d obs.	Live box	3		
	0.0	10.5-15.5	216-537 ^{‡1}	Artificial ^{§0}	Treble+*1,50	4-d obs.	Live box	27		1800
Chinook salmon	11.5		$405-750^{d}$	350	Single**	5-d radio telem.		17	Alaska	Bendock and
O. tshawytscha			750-1,210 ^d		Single**	5-d radio telem.		RU		Alexandersdottir
	8.9		590-1,155 ^d	Artificial ⁵⁰	Single**	5-d radio telem.		15		(1993)

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Table 1.	Communica.		8.		100 CO 10	8				
,	Mortality	Temp.	Length	·		Study design	ign			
Species	(%)		(mm)	Bait type	Hook type	Method	Environment	Z	Location	Reference
Atlantic salmon	0.3	9.0-16.0	19940	Artificial ⁵⁰	Treble*1	14-d obs.	Raceway	300	Maine	Warner (1976)
	2.7	9.0-16.0	194^{40}	Artificial ⁹⁰	Single**	14-d obs.	Raceway	300		
	4.6	9.0-16.0	19140	Artificial ⁹⁰	Single**	14-d obs.	Raceway	300	3	
	5.7	9.0-16.0	186^{40}	Natural ^{§1}	Single**	14-d obs.	Raceway	300		
Atlantic salmon	4.0	14.0-19.0	293-324 ^{‡0}	Artificial ⁵⁰	Single**	2-d obs.	Holding pen	111	Maine	Warner and Johnson
	35.0	14.0-19.0	293-32410	Natural ^{§1}	Single**	2-d obs.	Holding pen	100		(1978) Atlantic
salmon	12.0	17.2		Artificial ⁹⁰	Single**	5-d obs.	Holding pen	52	Maine	Warner (1978)
	26.0	17.2		Artificial ⁵⁰	Treble*1	5-d obs.	Holding pen	36<		
	15.0	17.2		Artificial ⁹⁰	Single**	5-d obs.	Holding pen	95		
	8.0	17.2		Artificial ⁹⁰	Treble*1	5-d obs.	Holding pen	116		
Atlantic salmon	73.0^{2}	16.1	233 - 328	Natural ^{§1}	Single*0	14-d obs.	Raceway	106^{4}	Maine	Warner (1979)
	6.0	13.3	233-32840	Artificial ⁸⁰	Treble*1	5-d obs.	Raceway	300		
	4.6	13.3	233 - 328 ^{‡0}	Artificial ⁵⁰	Single**	5-d obs.	Raceway	302		
	4.1	13.3	233-328 ^{‡0}	Artificial ^{§0}	<u>ــــــــــــــــــــــــــــــــــــ</u>	5-d obs.	Raceway	319		
	5.7	13.3	233 - 328 ⁴⁰	Natural ^{§1}	Single*0	5-d obs.	Raceway	300		
Atlantic salmon	12.0	16.0	<646 ^{‡0}	Artificial ⁸⁰	Single+#0.\$0	1.5-d obs.	Tank	25	Canada	Brobbel et al. (1996)
	0.0	4.0	<646 ^{‡0}	Artificial ⁵⁰	Single+#0,50	1.5-d obs.	Tank	24		
Atlantic salmon	40.0	20.0	$<646^{10}$	Artificial ^{§0}	í	12-h obs.	Tank	10	Canada	Wilkie et al. (1996)
Atlantic salmon	80.0	20.0	603 ^{‡1}		**	3-d obs.	Tank	rv	Canada	Anderson et al. (1998)
	0.0	16.5	25840		**	3-d obs.	Tank	R)		Ti di
	0.0	8.0	$628^{‡1}$			3-d obs.	Tank	9		
Atlantic salmon	0.0	13.0	580-1,100 ^{‡1}	Artificial ^{§0}	Treble+#1.50	42-d telem.		18	Norway	Thorstad et al. 2007
Brown trout	2.1	12.0	84-409to	Artificial ⁸⁰	Treble+#1,50	2-d obs.	Holding pen	26	Wisconsin	DuBois and Dubielzig
Salmo trutta	2.2	12.0	84-409 ^{‡0}	Artificial ⁵⁰	Treble-*1, \$1	2-d obs.	Holding pen	46		(2004)
	0.0	12.0	84-409	Artificial ⁵⁰	Single+#0, \$0	2-d obs.	Holding pen	35		
	5.3	12.0	84-409 ^{‡0}	Artificial ^{§0}	Single-#0, \$1	2-d obs.	Holding pen	38		
Brown frout	3.0	7.2-17.2	$144 - 526^{40}$	Natural ^{§1}	Single+#0.50	3-d obs.	Holding pen	89	Wisconsin	DuBois and Kuklinski
					ì		I S			(2004)
Brown trout	7.8	10.0 - 18.0	135-228	Natural ^{§1}	Single**	14-d obs.	Aquaria	200	New York	Hulbert and
	23.0	10.0-18.0	135-228#0	Natural ^{§1}	Single*0	14-d obs.	Aquaria	100		Engstrom-Heg (1980)
(1980)	12.0	10.0-18.0	$135-228^{40}$	Natural ^{§1}	Single#0	14-d obs.	Aquaria	100		
	13.0	10.0-18.0	135-228 ^{‡0}	Natural ^{§1}	Single ^{#0}	14-d obs.	Aquaria	100		
	11.0	10.0-18.0	135-228 ⁴⁰	$Natural^{\S 1}$	Single#0	14-d obs.	Aquaria	100		
Brown trout	6.0		91-39140	Artificial ⁹⁰	Single, treble	1-d obs.	Live crate	107	Michigan	Shetter and Allison
										(1958)

able 1.—Continued

	Mortality	Temp.	Length			Study design	m			
Species	(%)	(C)	(mm)	Bait type	Hook type	Method	Environment	Z	Location	Reference
Brown trout	0.0		76-302 ^{‡0}	Artificial ^{§0}	Single**	1-d obs.	Live crate		Michigan	Shetter and Allison
	20.3		76-302 ^{‡0}	$Natural^{\S 1}$	Single**	1-d obs.	Live crate	29	Michigan	(1955)
Brown trout	7.0	12.0-13.0		Natural ^{§1}		10-d obs.	Holding pen		South	Barwick (1985)
	3.0	12.0-13.0		Artificial ⁵⁰		10-d obs.	Holding pen	119	Carolina	6
Brook trout	3.1	5.6-17.8	<381 ^{‡0}	Artificia _{[50}	Single, treble+, -	2-d obs.	Holding pen		Michigan	Nuhfer and
S. fontinalis	8.0	5.6-17.8	>381 ^{‡1}	Artificial ^{§0}	Single, treble+, -	2-d obs.	Holding pen)	Alexander (1992)
Brook trout	8.6		114-278 ^{‡0}	Artificial ^{§0}	Treble+#1, \$0	2-d obs.	Holding pen	41	Wisconsin	DuBois and Dubielzig
	0.0		114-278 ^{‡0}	Artificial ^{§0}	Treble-#1, \$1	2-d obs.	Holding pen	33		(2004)
0.0		$114 - 278^{40}$	Artificial ⁹⁰	Single+#0,\$0		2-d obs.	Holding pen	30	14	
	0.0		114-278 ^{‡0}	Artificial ⁵⁰	Single_#0, \$1	2-d obs.	Holding pen	23		
Brook trout	7.0		103-304 ^{to}	Natural ^{§1}	Single+#0,50	3-d obs.	Holding pen	100	Wisconsin	DuBois and Kuklinski
	2.0	7.2-17.2	$103-304^{10}$	Natural ^{§1}	Single -*0, \$1	3-d obs.	Holding pen	66	12	(2004)
Brook trout	37.5		$122 - 241^{40}$	$Natural^{51}$	Single**	Mark-recapture	Stream channel	550	Michigan	Shetter and Allison
				-20	ľ.		PSI		ř.	(1955)
1985	1.7		$122 - 241^{40}$	Artificial ^{§0}	Single**	Mark-recapture	Stream channel	484		
	54.2		76-25140	Natural ^{§1}	Single**	1-d obs.	Live crate	24		
	42.9		76-25140	Natural ^{§1}	Single**	1-d obs.	Live crate	21		
	4.3		76-251 ^{to}	Artificial ^{§0}	Single**	1-d obs.	Live crate	23		
	3.0		$102 - 302^{40}$	Artificial ^{§0}	Single**	1-d obs.	Live crate	135		
	35.3		$102 - 302^{‡0}$	Natural ^{§1}	Single**	1-d obs.	Live crate	102		
	56.7		$102 - 302^{40}$	Natural ^{§1}	Single#0	1-d obs.	Live crate	30		QT.
Brook trout	5.6	-	74-300 ^{‡0}	Artificial ⁵⁰	Single, treble	1-d obs.	Live crate	908	Michigan	Shetter and Allison
									ĺ	(1958)
Brook trout	8.8			$Natural^{\S 1}$	Single+#0,50			400	Michigan	Westerman (1932)**
	2.8			Artificial ^{§0}	Single+#0,50			400	í	
Brook trout	0.0	10.0	275^{40}	Sim. angling	1		Tank	12	New York	Schreer et al. (2005)
Brook trout	27.123	1.6-8.2	233^{40}	Naturals	Single+*0.50	42-d obs.	Raceway	100	Wisconsin	Dubois and Pleski
	32.923	1.6-8.2	233^{40}	Natural ^{§1}	Single-#0.51	42-d obs.	Raceway	100		2007
Lake trout	14.9	4.0-20.0	461-801	Artificial ⁵⁰	Single, treble	42-d obs.	Buoy system	29	Michigan	Loftus et al. (1988)
S. namaycush									22	
Lake trout	11.7	<12.0	259-889	Artificia] ⁵⁰	Treble*1	Telemetry		17	Colorado	Lee and Bergersen
	87.5		635-838	Artificial ⁵⁰	Treble*1	Telemetry	The second of th	œ		(1996)
Lake trout	10.0	1.0-3.0	250-423	Natural ^{§1}	Single+*0,50	2-d obs.	Holding pen	22	Canada	Dextrase and Ball
										(1751)

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		September 1	i i	A80						
W	Mortality		Length			Study design	gn			
Species	(%)	(C)	(mm)	Bait type	Hook type	Method	Environment	Z	Location	Reference
Lake trout	32.0	Ice cap Ice cap	475	Natural ^{§1} Artificial ^{§0}	Single#0 Single, treble	12-d obs.	Holding pen	33	Minnesota	Person and Hirsch
Lake trout	6.9	•	320-960	Artificial ^{§0}	Treble+#1, \$0		10	72	Canada	Falk et al. (1974)*/**
Lake trout	7.0 7.11		320-960	Artificial ⁸⁰ Artificial ⁸⁰	Treble*1, \$1 Treble**, \$0			27		Nadom (1009)***
Salvelinus sp.	6.04		274	Artificial ⁸⁰	HEDICT	2-d obs.	Live box	157	Colorado	Naueau (1962) Klein (1966)
Whitespotted char S. leucomaenis	ar 0.1	8.2–16.4	96–31°	Natural ^{§1}	Single+*0, \$0	Mark-recapture			Japan	Tsuboi and Morita (2004)
Esocidae										
Northern pike	33.3	Ice cap	495 ^{‡0}	Natural ^{§1}	"Swedish hook"	2-d obs.	Holding pen	24	Wisconsin	DuBois et al. (1994)
Esox lucius	9:0	Ice cap	45540	Natural ^{§1}	Treble#1	2-d obs.	Holding pen			
Northern pike	0.0		509-1,087 ^{‡1} 485-939 ^{‡1}	Artificial ⁸⁰ Artificial ⁸⁰	Single, treble-51 Single treble-51	2-d obs.	Holding pen	31 5	31 ✓ Alaska	Burr (1998)
Northern nike	2.5		212 00111	Artificial ⁸⁰	Single, treble	Multiple control	Dendang pen			
Northern pike	6.4	19.0	365-880 ^{‡1}	Atumenal	Jreble+, -#1,50	Mumple capture	rona	3	Canada	Falk and Gillman
Esox sp.	11.75				(A)	1-d obs.	Holding pen	388	Illinois	(19/5)* Storck and Newman (1992)
Esox sp.	9.75				**	1-d obs.	Holding pen	217	Illinois	Newman and Storck
Muskellunge F masaninonan	30.0		619–918	Artificial ^{§0}		3.5-d obs.	Respirometer	52	Canada	Beggs et al. (1980)
Muskellunge		21.0-23.0	413	$Natural^{\S 1}$	Single+#0,50	1-d obs.	Pond	85	Illinois	Ostrand et al. (2006)
Muskellunge	83.0	2000		Natural ^{§1}	Single+#0,50	2 years rearing	Pond		Wisconsin	Margenau (2007)
rear ab.	7.7	13.0-63.0	730-300	Armicial	redie+		Pond	2 8	Missouri	Weithman and Anderson (1976)
Percidae									80	
Sauger Sander canadensis ^c	4.0-12.0	10.0	220-475	Artificial ⁹⁰	Single, treble	Telemetry	Holding pen	. 6	Tennessee	Bettoli et al. (2000)
Zander S. lucioperca	8.0-47.0	10.0	<500 ^{‡0}	Air exposure	e e	40-d obs.	Ponds	107	Germany	Arlinghaus and Hallermann (2007)
i i										

Table 1.—Continued.

	Mortality	Temn	Ipnoth			Shidy design	Lou			
Species	(%)		(mm)	Bait type	Hook type	Method	Environment	N	Location	Reference
Walleye S nitroush	1.1	8.0-11.0	275-577	Artificial,		12-d obs.	Holding pen	180	Washington	Fletcher (1987)
Walleye	5.0	13.0-28.0	289–600	Artificial,	Single, treble+50	Mark-recature	Pond	839~	839 V Minnesota	Payer et al. (1989
Walleye	22.8	8.3-11.1	>381			3-d obs.	Holding pen	75	South Dakota	South Dakota Fiedler and Johnson (1994)
Walleye Walleye	40.0	13.0-14.0	100			5-d obs. 68-h obs.	Holding pen	161 < 75 <	Minnesota South Dakota	9
a farming	15.0	14.0				68-h obs.	Tank	757		
Walleye	0.8	16.0-20.0		Artificial,	Single, treble+, -	2-d obs.	Live box	240	Canada	Schaefer (1989)
Walleve	57.43	24.0-26.0				Carcass obs.	Lake	2,701	Wisconsin	Hoffman et al. (1996)
Walleye	0.0	10.0-26.3	203-762		Single+*0.50	120-h obs.	Holding pen	204	Minnesota	Reeves and
•	3.5	10.0-26.3	203-762		Single+*0.50	120-h obs.	Holding pen	473	S _C	Brusewitz (2007)
	12.2	10.0-26.3	203-762		Single+#0.50	120-h obs.	Holding pen	406		
	5.6	10.0-26.3	203-762		Single+#0.50	120-h obs.	Holding pen	2		
(8)	0.0	10.0-26.3	203-762		Single+#0.50	120-h obs.	Holding pen	2		
Sander sp.	0.0	21.0	258-687		Single**					Parks and Kraai
r	39.47	22.0-24.0	258-687		Single*0	lugar.				(1991)*
	80.0	24.0-27.0	258-687		Single*0					***************************************
Yellow perch Perca flavescens	20.0 ^{8, 10} 2.0 ^{9, 10}	18.2–20.3 18.2–20.3							Illinois	Kenury et al. (1996)
Cyprinidae	i	9							NT other land	Bank at a1 (1007)
Common bream	016.01	12.0-18.0	·						Ivemenanas	Naat et al. (1997)
Common carp	2.0^{10}			Natural ^{§1}					Netherlands	Beukema (1970)
Cyprinus carpio	c L	0 00		. 14			,	5	Motherlands	Dast (109E)
Common carp	3.0	18.0-22.0	341t	Natural st Natural st		22-d angling	Fond	13 611	ivenienalius	Nadi (1762)

tality studies with deeply hooked fishes; ³ = mortality calculated according to Wilde (1998); ⁴ = data correspond to salmonid hybrids Salvelinus fontinalis × S. namaycush; ⁵ = data correspond to esocid hybrids Esox masquinongy × E. lucius; ⁶ = data correspond to 38 esocid species (9 muskellunge and 12 hybrids); ⁷ = data * = previously Salmo clarkii; b = previously Stizostedion vitreus; c = previously Stizostedion canadense; d = mideye length; c = fork length; 2 = hooking morcorrespond to percid species (walleye and sauger); 8 = gas bladder not punctured; 9 = gas bladder punctured; 10 = no hooking mortality study.

Table 2.—Length limit key applied for assigning undersized and legal-sized fish. The most common minimum-size limit applied in Germany was used. Only these species were included in the fish size analysis in the present paper.

Fish species mentioned in German fisheries bylaws	Minimum-size limit
Common carp Cyprinus carpio	350 mm
Northern pike Esox lucius	500 mm
Rainbow trout Oncorhynchus mykiss and cutthroat trout O. clarkii	250 mm
Atlantic salmon Salmo salar	600 mm
Brown trout S. trutta	250 mm
Brook trout Salvelinus fontinalis	300 mm
Zander Sander lucioperca	450 mm

to the consumptive nature of German recreational fisheries that promotes removal of the smallest size-classes of mature fish species. Due to the lack of assignability of divergent minimum-size limits of European to non-European fish species (e.g., it would be unwise to assign a minimum-size limit of northern pike Esox lucius to muskellunge E. masquinongy), we excluded non-European species from the calculation of fish length as a determinant of hooking mortality in the current study (see Table 2 for species included in this analysis). Terminal gear used in each study was grouped into artificial bait (lure, spoon, spinner, and fly) and natural bait (worm and baitfish). The hooks, which were used in the experiments in the different studies, were classified into single and treble hooks and into barbed and barbless hooks.

The statistical analysis was conducted assuming independence of each hooking mortality estimate extracted from the primary literature (Taylor and White 1992). To compare the average hooking mortality between species groups, the analysis was first descriptively conducted for the entire data set. Then, differences between the groups of salmonid and percid species were calculated. Because of a lack of an adequate sample size of mortality estimates, the Esocidae and Cyprinidae were excluded from the family-specific analyses. A finer scale breakdown to the level of the individual species was not possible due to small sample size. For statistical analysis of hooking mortality rates and determinants of hooking mortality, percent mortality was arcsine square root-transformed according to Zar (1996). We tested the effect of the five potential determinants of hooking mortality across all species and specifically for

Salmonidae and Percidae using a factor-specific approach similar to Bartholomew and Bohnsack (2005). Missing values were too high for some factors to allow a multivariate analysis of the impact of all five potential determinants of hooking mortality simultaneously; therefore, univariate analysis on the determinants of hooking mortality was conducted for each of the five determinants separately.

Spearman's rank correlations were conducted to determine the influence of water temperature on hooking mortality. One-way analysis of variance (ANOVA) and t-tests were used to investigate differences of hooking mortality between fish families and between different levels of nominally coded determinants of hooking mortality (e.g., barbed versus barbless hooks). For ANOVAs, a Tukey-HSD post hoc test at homogenous variances between factors and a Dunnett's T3 post hoc test at heterogenous variances were used. To test the homogeneity of variances, Levene's tests were conducted. All statistical analyses were conducted with SPSS (Statistical Package for the Social Sciences) version 13.0. Threshold of significance in all tests was $\alpha = 0.05$.

Results

Descriptive Data

We identified n = 107 individual hooking mortality studies. From these studies, n = 252 individual estimates of hooking mortality for n = 8 European fishes and n = 10 species from the same genus were compiled. The greatest number of hooking mortality estimates was identified for Salmonidae (n = 213), followed by Percidae (n = 22), Esocidae (n = 12), and Cyprinidae

(n = 5). Most mortality estimates (27%) were available for rainbow trout (n = 67) followed by cutthroat trout (n = 26), Chinook salmon (n = 26), and Atlantic salmon Salmo salar (n = 25) (Table 3). The former species are not all native to Europe, but, for example, rainbow trout was introduced in the late 19th century and is today a popular recreational fish species in many European countries.

Mean hooking mortality across species was 15.9%, the median was 7.8% and the range 0–88.5% (see Table 3 for measures of variance). Most estimates of hooking mortality were low, with 57.1% of all hooking mortality values below 10%, 15.9% between 10 and 20%, 8.0% between 20% and 30%, and 19.0% greater than

30%. Only 7.9% of all hooking mortality estimates were greater than 50%.

Average hooking mortality was highest for Percidae (19.9%) followed by Salmonidae (15.9%), Esocidae (14.9%), and Cyprinidae (5.7%) (see Table 3 for measures of variance), but these differences were not significant (F = 0.528, df = 3, P = 0.664). Within the Salmonidae, the highest average mortality was found in coho salmon (27.4%), followed by lake trout Salvelinus namaycush (21.2%), Chinook salmon (21.2%), rainbow trout (17.1%), and Atlantic salmon (14.6%) (Table 3). Within Percidae, the highest average mortality was determined for zander (27.5%). Average mortality was considerably higher for muskellunge (30.7%) than

Table 3.—Descriptive data of hooking mortality estimates of native European fish species and nonnative fish species from the same genus (called related).

Family	Species	Attribution	n (studies)	n (estimates)	mean ± SE (%)
Salmonidae	Arctic grayling Thymallus articus	Related	2	8	3.0 ± 1.6
	Coho salmon Oncorhynchus kisutch	Related	6	13	27.4 ± 6.6
	Rainbow trout O. mykiss	Nativea	24	67	17.1 ± 2.6
	Cutthroat trout O. clarkii	Related	7	26	11.1 ± 3.9
	Chinook salmon O. tshawytscha	Related	9	26	21.2 ± 3.7
	Atlantic salmon Salmo salar	Native	12	25	14.6 ± 4.3
	Brown trout S. trutta	Native	6	15	7.4 ± 1.9
	Brook trout Salvelinus fontinalis	Native*	8	22	15.4 ± 4.0
	Lake trout S. namaycush	Related	6	9	21.2 ± 8.7
	Salvelinus fontinalis \times S. namaycush	Related	1	1	7.0
	Whitespotted char S. leucomaenis	Related	1	1	0.1
	Mean		82	213	15.9 ± 1.4
Esocidae	Northern pike Esox lucius	Native	4	6	7.1 ± 5.3
	Muskellunge E. masquinongy	Related	4	4	30.7 ± 18.5
	Esox lucius × E. masquinongy	Related	1	1	11.7
	Diverse Esox species	Related	1	1.	1.7
	Mean		10	12	14.9 ± 7.0
Percidae	Zander Sander lucioperca	Native	1	1.	27.5
	Sauger S. candensis	Related	1	1	8.0
	Walleye S. vitreus	Related	8	15	17.5 ± 6.1
	Sander vitreus \times S. canadensis	Related	1	3	39.8 ± 23.1
	Yellow perch Perca flavescens	Related	1	2	11.0
	Mean	**	12	22	19.9 ± 5.3
Cyprinidae	Common bream Abramis brama	Native	1	2	9.3
	Common carp Cyprinus carpio	Native	2	3	3.3 ± 0.9
	Mean		3	5	5.7 ± 1.6
Total			107	252	15.9 ± 1.3

^{*} Formerly introduced to Europe but nowadays identified as native in some countries such as Germany.

for northern pike (7.1%). Cyprinidae, common carp *Cyprinus carpio*, and common bream *Abramis brama* were characterized by a low-average hooking mortality (<9.3%), but sample size was low.

Determinants of Hooking Mortality

All species.-Water temperature was significantly positively related to overall hooking mortality across all species (Spearman rank correlation, $\rho = 0.165$, P = 0.037, n = 161). Hooking mortality did not depend on size of fish comparing average mortality of undersized and legalsized fish (Table 4). However, there was a significant difference in the average mortality of fish captured on artificial lures (11.4%) compared to those captured on natural bait (25.9%, see Table 4 for measures of variability). Mortality was significantly higher for fish captured with barbed hooks (14.6%) compared to fish caught with barbless hooks (8.2%). Across all species, type of hook (single or treble) did not influence the level of hooking mortality (Table 4).

Salmonidae.—Water temperature positively and significantly correlated with hooking mortality in salmonids (ρ = 0.254, P = 0.003, n = 132). Similarly to the analysis using the entire data set, average mortality did not differ between undersized and legal-sized salmonids (Table 4). However, mortality caused by artificial angling baits (11.6%) was significantly lower compared to natural baits (27.0%). Within the salmonid family, hooking mortality did not vary with hook type, but average mortality of Salmonidae caught on barbed hooks (15.1%) was significantly higher than for fish caught on barbless hooks (8.6%).

Percidae.—Water temperature ($\rho = 0.183$, P = 0.415, n = 22) was unrelated to hooking mortality in Percidae. All comparisons of determinants were not assessed due to low sample size (Table 4).

Discussion

Our study represents the first compilation of hooking mortality estimates for European freshwater or diadromous fish species and their relatives within the same genus. The great popularity of catch and release in recre-

ational fisheries and the need to release undersized or otherwise protected fish in almost all recreational fisheries in Europe increases the importance of understanding and minimizing catch-and-release-related hooking mortality. To achieve the basic assumption of catch and release—that released fish survive the capture event unharmed-it is indispensable to study the determinants of hooking mortality and use this knowledge to improve handling techniques and thereby increase survival (Arlinghaus et al. 2007a, 2007b). Using a different data set, our results were found surprisingly similar to many of the insights from an earlier meta-analysis by Bartholomew and Bohnsack (2005). Hence, some level of generalization across species and ecological environments (e.g., freshwater versus saltwater) on the determinants of hooking mortality may be possible. However, the great variability in hooking mortality across species identified in our study and in previous reviews (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Cooke and Suski 2005) indicates that such generalization must be conducted with care.

Our data supported the meta-analysis by Bartholomew and Bohnsack (2005) in terms of the overall highly skewed distributional pattern of hooking mortality estimates across species, with most estimates being low and only few outliers present. We found an average hooking mortality across all species of 15.9%, which is slightly lower than the average value for all species (18%, including marine) reported by Bartholomew and Bohnsack (2005). Similarly, our median value of 7.8% was lower than the median (11%) reported by Bartholomew and Bohnsack (2005). The wide range of mortality estimates reported in the present paper (0-88.5%) agreed well with the review by Muoneke and Childress (1994), which resulted from a limited set of studies with unusually high hooking mortality reports. The mentioned exceptional high hooking mortality rates were caused in deeply hooked fish (Mason and Hunt 1967; 88.5%) or where fish were caught in very unfavorable (mostly high) water temperatures (e.g., Parks and Kraai 1991, 80.0%; Graeb et al. 2005, 79.0%).

The significant positive relation between water temperature and hooking mortality identified by Bartholomew and Bohnsack (2005)

Table 4.—Mean hooking mortality (±SE) caused by four variables across all species and specific for Salmonidae and Percidae.

Variable	All species Mean \pm SE (n)	Statistics	Salmonidae Mean \pm SE (n) Statistics	Statistics	Percidae Mean ± SE (n) Statistics	Statistics
Length ^a Undersized Legal length	$15.4 \pm 2.3 (80)$ $11.2 \pm 2.8 (45)$	t = 1.44, df = 123, P = 0.151	15.4 ± 2.5 (76) 12.3 ± 3.2 (40)	15.4 ± 2.5 (76) $t = 0.99$, df = 114, $P = 0.321$ 12.3 ± 3.2 (40)	27.5 (1) (0)	· •
Bait type Artificial bait Natural bait	$11.4 \pm 1.3 (142)$ $25.9 \pm 3.3 (53)$	t = -4.15, df = 73.85, P < 0.000	$11.6 \pm 1.4 \ (136)$ $27.0 \pm 3.4 \ (46)$	t = -4.46, df = 64.42 , $P < 0.000$	8.0 (1)	ሳ
Hook type Single hook Treble hook	$15.9 \pm 1.8 (120)$ $11.7 \pm 2.4 (47)$	t = 1.20, df = 165, $P = 0.232$	$15.4 \pm 1.7 (110)$ $12.4 \pm 2.6 (44)$	t = 0.97, df = 152, $P = 0.332$	7.2 ± 10.1 (8) - (0)	ሳ .
lype of barb Barbed Barbless	$14.6 \pm 2.6 (57)$ $8.2 \pm 1.9 (42)$	t = 2.01 df = 96.99, P = 0.047	$15.1 \pm 2.6 $ (48) $8.6 \pm 2.0 $ (40)	t = 2.00, df = 86, $P = 0.048$	3.9 ± 1.8 (6) – (0)	å

^a Comprised hooking mortality estimates of rainbow trout, cutthroat trout, Atlantic salmon, brown trout, brook trout, northern pike, zander, and common carp according to the stated minimum size limits.

^b Statistical tests not possible due to small sample size.

was confirmed in the present study across all species and for Salmonidae. The increasing probability of death after release with warming water has been repeatedly described for many recreational fish species, including various salmonid fish species (Arlinghaus et al. 2007b). For example, in rainbow trout, Dotson (1982) found an increased hooking mortality from 0% to 8.6%, with an increase in water temperature from 8.3°C to 16.1°C. Unfortunately, Bartholomew and Bohnsack (2005) only contrasted "cool" and "warm" water temperature but did not identify thresholds between these two categories. Previous studies on a variety of species determined species-specific water temperature thresholds (Hoffman et al. 1996; Graeb et al. 2005; Reeves and Brusewitz 2007). Above these thresholds, hooking mortality sharply increases (Hoffman et al. 1996; Wilkie et al. 1997; Dempson et al. 2002; Graeb et al. 2005). For example, in a review in Atlantic salmon, Thorstad et al. (2003) reported a sudden mortality increase at water temperatures greater than 18°C (see also Wilkie et al. 1997; Dempson et al. 2002), whereas mortality was low between water temperatures ranging from 8°C to less than 18°C. Also, Anderson et al. (1998) showed a temperature threshold for hooking mortality in Atlantic salmon. They found 0% hooking mortality for salmon captured and release at 8°C and 16.5°C and strongly increased hooking mortality of 80.0% for a water temperature of 20°C. Analogous to Salmonidae, hooking mortality has been found to increase strongly with increasing water temperatures in various Esocidae and Percidae (Storck and Newman 1992; Hoffman et al. 1996; Wilde et al. 2000; Graeb et al. 2005). The difference in hooking mortality at high and low water temperature probably reflects increased physiological stress responses at higher temperatures for most cold- or coolwater adapted fish species (Wydoski et al. 1976; Gustaveson et al. 1991; Wilkie et al. 1997). Furthermore, fish have a particularly high requirement for dissolved oxygen at high water temperature, which increases when they are stressed by the catch-and-release event at high water temperature (Portz et al. 2006). Also, there is potential for increased speed of infections of hooking wounds at higher water temperature (Muoneke 1992), which collectively explains the significantly positive relationship

between water temperature and hooking mortality found in the present meta-analyses and in various earlier reports cited above.

Similar to the meta-analysis by Bartholomew and Bohnsack (2005), we did not detect a differential mortality of legal and undersized fish. Because we classified fish sizes into two categories (i.e., smaller or larger than a "typical" minimum-size limit), our results can only cautiously be compared with literature reports. Obviously, minimum-size limit regulations differ across the world, even from one water body to the other (Paukert et al. 2001). Nevertheless, we considered the classification into legal and sublegal fish useful because the success of any form of minimum-size limit depends on the high survival rate of undersized fish being released mandatorily. The lack of relation between fish size and hooking mortality in the present study agreed various previous studies for different fish species (Klein 1966; Warner and Johnson 1978; Storck and Newman 1992; Schill 1996; Dedual 1996; Bartholomew and Bohnsack 2005), but there are also contradictory findings in various recreationally important fish species (e.g., Loftus et al. 1988; Wertheimer 1988; Bendock and Alexanderdottir 1993; Schisler and Bergersen 1996; Burr 1998; Reeves and Brusewitz 2007). Giving these findings and despite the lack of significant relation between "legal" and "undersized" fish and hooking mortality in the present meta-analysis and the lack of a differential mortality for small and large fish in Bartholomew and Bohnsack (2005), there seems to be little room for generalization about the influence of fish size and hooking mortality. However, the important message is that if water temperature is not critical and injury rates are low and handling is appropriate (e.g., low level of air exposure and quick hook removal), undersized fish (i.e., likely immature and small individuals) can have a similar survival probability to legal-sized fish (i.e., likely mature and large individuals). These are good news for fisheries manager interesting in saving immature fish from death using appropriately high minimum-size regulations in European recreational fisheries.

We found, in analogy to Bartholomew and Bohnsack (2005), that European fish species captured on natural bait exhibited a significantly higher hooking mortality than those

captured on artificial bait. The coherence between natural baits and high hooking mortality was true across all fish species and specifically for salmonids. Similar findings have been previously reported. For example, in Atlantic salmon, Warner and Johnson (1978) reported a hooking mortality of 35% for fish captured on natural bait (worm) and a hooking mortality of only 4% for fish captured with artificial bait (fly). Similarly, Payer et al. (1989) found that walleye caught with live natural bait suffered from a higher hooking mortality (10%) than walleye captured with artificial lures (0%). Previous reviews identified anatomical hooking location and the injury of lethal organs as the most important factor of hooking mortality for most fish species (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005). Fish typically ingest natural bait more deeply than artificial bait (Muoneke and Childress 1994), which was documented for various salmonids (Warner 1976; Warner and Johnson 1978; Taylor and White 1992), percids (Payer et al. 1989), and esocids (DuBois et al. 1994; Arlinghaus et al. 2008). Deep hooking not only increases the hook removal times, and thus air exposure, but also increases the likelihood of bleeding and lethal injury (Arlinghaus et al. 2008), which is known to correlate strongly and positively with hooking mortality in fish (Payer et al. 1989; DuBois et al. 1994; Person and Hirsch 1994).

We did not detect a significant relation between type of hook (single versus treble) and hooking mortality in our meta-analysis, which is in agreement with findings by Bartholomew and Bohnsack (2005) and also corresponded with an earlier meta-analysis by Taylor and White (1992) for salmonids. However, inconsistencies in research results remain. Some previous research has shown that treble hooks caused less mortality compared to single hooks because they hook the fish shallower (Muoneke and Childress 1994; e.g., in rainbow trout, brown trout Salmo trutta, lake trout [Klein 1965; DuBois and Dubielzig 2004], coho salmon, Chinook salmon [Gjernes et al. 1993], sauger [Bettoli et al. 2000], and northern pike [DuBois et al. 1994]). By contrast, Jenkins (2003) found no differences in hooking location of single and treble hooks in rainbow trout. The effect of hook type on hooking mortality seems largely species-specific and may depend on the size of

the hook relative to the gape of the fish. Moreover, the type of fishing (active versus passive) and the specific foraging behavior of the fish will determine hooking location of either single or treble hooks (Schisler and Bergersen 1996). The demonstrated complexity in hook type-related mortality and the possibility of confounding variables such as fishing technique that was uncontrolled in the present meta-analysis probably explains the lack of a generally significant relation between hook type and hooking mortality in this study.

Our research sheds some more light on the conservation value of barbless hooks compared to barbed hooks (Taylor and White 1992; Schill and Scarpella 1997; DuBois and Dubielzig 2004; DuBois and Kuklinski 2004; Meka 2004). Our study has similar results to Bartholomew and Bohnsack (2005), who also reported that barbless hooks caused less hooking mortality compared to barbed hooks across various fish species. Higher mortality caused by barbed hooks could be related to increased level of injury and bleeding (Gjernes 1993; Muoneke and Childress 1994; Meka 2004; DuBois and Pleski 2007). Moreover, removal of barbed hooks may be more time consuming and increase air exposure and physiological stress levels in fish (Cooke et al. 2001). However, our findings contrast with Wydoski (1977), Schill and Scarpella (1997), DuBois and Dubielzig (2004), and DuBois and Kuklinski (2004), who reported that the use of barbed or barbless hooks has no influence on hooking mortality and is rather a "social issue" (Schill and Scarpella 1997). While we cannot discount the possibility that the significant relationship between barbed hooks and hooking mortality in the present work is spurious and potentially a result of an uncontrolled confounding variable (e.g., fish size and temperature), our findings support the idea that there might be some conservation value in using barbless hooks.

Hooking mortality is affected by more factors than we describe in the present study (see Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007b for a complete list). Further determinants are for instance anatomical hooking location, water depth where fish are caught, and level of air exposure and handling time, and there can of course be various interactive effects (e.g., between air exposure and temperature; Gingerich et al. 2007). Gingerich et al.

(2007) stated that the determinants of hooking mortality in the context of recreational fishing were often studied independently. The authors highlighted the importance of interactive effects using the example of air exposure. duration and water temperature on survival of bluegill. They showed that mortality strongly increased with increased air exposure duration and high water temperature. However, at low to moderate water temperatures, high air exposure durations did not result in high mortality rates. Due to lack of sample size, we were unable to study such or other interactive effects, nor could we conduct multivariate analyses controlling for the individual effect of selected determinants. Thus, there remains a need for increased research on interactive effects of various factors on hooking mortality, and insights from such research can moderate the findings reported here and in Bartholomew and Bohnsack (2005) for individual hooking mortality determinants.

In terms of further limitations of our study, much previous research on hooking mortality has been conducted under controlled conditions in holding pens or cages (Table 1). In addition to the fundamental issue of many studies lacking appropriate control fish (Pollock and Pine 2007), which may have influenced the results of the present study due to inclusion of all identified hooking mortality studies irrespective of their quality, there seems to be a heavy focus towards estimating initial hooking mortality defined as immediate mortality at capture up to 24 h postcapture (e.g., Bouck and Ball 1966; Mason and Hunt 1967). By contrast, delayed mortality defined as mortality happening 24 h up to several weeks after the capture-and-release event (e.g., Wilde 1998) is normally not estimated for methodological reasons. We used the category of total mortality (Wilde 1998) in our analysis, but we must be reminded that in many cases, no estimate of delayed mortality was available. This might have influenced the result of the present metaanalysis. Estimating delayed mortality after catch-and-release fishing using appropriate technology such as catching and releasing previously tagged and fully recovered individuals (either using acoustic or radio tracking; see Donaldson et al. 2008) constitute an important research and management issue for the future because this mortality is often not detected in the routine practice of releasing fish, which may defeat the underlying objective of many harvest regulations in recreational fisheries (Coggins et al. 2007).

Our literature review and Arlinghaus et al. (2007b) has highlighted the limited research on native European fish species in the context of catch and release, and among the available research there has been a heavy focus on salmonids. Development of sustainable management of European recreational fish species demands increased knowledge about the determinants of hooking mortality for the many generally understudied European fish species of recreational importance. In Table 5, a compilation of major research needs in the context of catch and release for European species is presented. For example, although small cyprinids and also common carp are almost exclusively catch-and-release fisheries in some countries (e.g., United Kingdom, North 2002; Arlinghaus 2007), there is little information available on the determinants of hooking mortality on small-bodied cyprinid species such as roach Rutilus rutilus or rudd Scardinus erythrophthalmus. Further research should not only be conducted on hooking mortality and its determinants (e.g., handling techniques and hook types and sizes) in a variety of European fish species (Table 5), but should also include the emerging field of the sublethal impacts of catch and release and associated practices such as retention in keep nets, so-called carp sacks, or lines (in European catfish Silurus glanis) on physiology, behavior, and reproductive output and fitness (Cooke et al. 2002; Arlinghaus et al. 2007b). Moreover, there is a need to analyze the interactive effect of various stressors on survival and sublethal reactions of European fish species to its full extent. Among these, one challenge stands out—to tackle the emerging question of barotrauma (Nguyen et al. 2009; Schreer et al. 2009; Wilde 2009) in percid fishes such as zander and Eurasian perch Perca fluviatilis, which can happen at comparatively shallow capture depth of several meters (see Shasteen and Sheehan 1997; Morrissey et al. 2005; Gravel and Cooke 2008; Schreer et al. 2009) and might be strongly mediated by water temperature and other as yet unresolved factors.

Table 5.—Summary hooking mortality research and future research needs of species of importance in European recreational fisheries. Level of knowledge is classified from deficient to excellent, with a medium category.

Family	Species	Level of knowledge	Future research needs
Salmonidae	Grayling Thymallus thymallus	Deficient	There are no hooking mortality studies on grayling. Detailed experiments on grayling should be conducted to evaluate the effects of catch-and-release recreational fisheries on this highly important
32	Rainbow trout	FreeMant	recreational fish species, alongside important determinants of hooking mortality such as water temperature and hooking location.
	Oncorhynchus mykiss	Excellent	A comprehensive amount of hooking mortality studies in rainbow trout is available. Future research on rainbow trout may focus on the interactive effects of multiple angling-induced stressors on hooking mortality (e.g., handling techniques at different wate temperatures).
	Atlantic salmon Salmo salar and brown trout S. trutta	Median	There are moderate amounts of studies on <i>Salmo</i> spp. Gear research, handling techniques and research on the fitness impacts of catch and release is warranted as well as studies on
			interactive effects on hooking mortality. For lake-dwelling brown trout forms in deep lakes, barotrauma research is needed.
	Brook trout Salvelinus fontinalis andArctic char S. alpinus	Median/ deficient	The recommendations for future research in <i>Salvelinus</i> spp. are identical to those given for <i>Salmo</i> spp. Note that no catch-and-release study have been conducted on Arctic charr, with one exception in the gray literature by McKinley (1993).
	Danube salmon Hucho hucho	Deficient	For Danube salmon, no catch-and-release studies exist although conservation of this species is an important fisheries management issue.
Esocidae	Northern pike Esox lucius	Median	The knowledge about the consequences of catch-and-release in northern pike needs extension. Current knowledge is mainly U.Sbased, with few exceptions (Arlinghaus et al. 2008, 2009; Klefoth et al. 2008). However, northern pike angling is popular in European recreational fisheries. One major field of research is the impact of water temperature in this

Table 5.—Continued.

Family	Species	Level of knowledge	Future research needs
,			mesothermal species. Research on pike should encompass the effect of the environment (e.g., salinigy in brackish water) as well as size of fish and related handling practices (e.g., vertical hold) on the survival and recovery after release.
Percidae	Zander Sander luciperca	Deficient	No research on the determinants of catch and release has been conducted in European zander, with one exception under pond conditions by Arlinghaus and Hallermann (2007). An overall need for catch-and-release studies exists because of the great popularity of this species in European recreational fisheries, in particular focusing on sublethal stressors, handling, and barotrauma in this
	Eurasian perch Perca fluviatilis	Deficient	physoclist. Currently, there is no hooking mortality available for this important fish
	jinominis		species. Besides research on the general determinants of hooking mortality and sublethal endpoints, w propose studying the impact of capture depth on this physoclistic species (e.g. Keniry et al. 1996).
Cyprinidae	Large-sized cyprinides (e.g., common carp Cyprinus carpio and asp Aspius aspius)	Deficient	Recreational fishing for carp is very in Europe (Arlinghaus 2007). Only a few catch-and-release studies on common carp are available (e.g., Rap et al. 2008), and no research on asp is available. Research needs encompasses studies on behavioral and growth impacts of this practice, as well as the impact of multiple recaptures because trophy carp are recaptured multiple times throughoutheir lifetime.
	Medium- and small-sized cyprinids (e.g., common bream Abramis brama, barbel Barbus barbus, silver bream A. bjoerkna, crucian carp Carassius carassius, European chub Leuciscus cephalus, ide L. idus, roach Rutilus rutilus, rudd Scardinus erythrophthmalus, and tench Tinca tinca)	Deficient	There is currently only very little research conducted on the lethal and sublethal impacts associated with catch and release, mostly focusing or the widespread usage of keepnets in recreational coarse fisheries for cyprinids (Raat et al. 1997; Pottinger 1998; Gallardo et al. 2009). These keepnets are used to hold fish during tournaments and other type of coarse fishing all over Europe, and there is a need to evaluate further the impact

Table 5.—Continued.

Tamily	Canadan	Level of	F. (
Family	Species	knowledge	Future research needs
9	* * * * * * * * * * * * * * * * * * *		of this type of retention along with evaluation of various forms on survival postrelease. Anecdotal evidence suggests that warmwater mortality of roach is very high, but
13	an an		this assumption needs to be investigated further, including analysis of various handling
Siluridae	Wels catfish <i>Silurus glanis</i>	Deficient	techniques without retention and prior to release (e.g., wet hands, dry hands) on disease outbreak and fungus infections postrelease.
Jamaac	veis canisi ourus gums	Dencient	There are no hooking mortality studies on European catfish. An overall need for catch-and-release studies exists because of the very popular trophy fisheries for wels catfish in Europe. Catfish anglers often use "lining" for trophy fish overnight. There is a need for studies to evaluate this practice in terms of hooking mortality and behavioural change postrelease.
Lotidae	Burbot <i>Lota lota</i>	Deficient	Currently, there are no catch-and-release-related mortality studies on burbot available. Research needs exists for all aspects of catch and release on burbot because of the popularity of this freshwater species in European recreational fisheries during the cold season and in deeper lakes.
Centrarchidae	Largemouth bass Micropterus salmoides	Excellent	The knowledge on catch-and-release fishing of largemouth bass is excellent. In southern Europe (Italy, Spain, and some regions in France) largemouth bass was introduced and is nowadays a popular game fish. In spite of the great amount of knowledge on catch and release in North America (e.g., Hanson et al. 2007; Siepker et al. 2007; Thompson et al. 2008; White et al. 2008; Siepker et al. 2009), there is a need to study
			the interactive effects of different determinants of hooking mortality ir catch-and-release <i>Micropterus</i> spp. fisheries (see Gingerich et al. 2007).

Management Implications

The live release of fish is useful to conserve and sustainable manage recreational fisheries, and it is a practice associated with all forms of size-based harvest limits (Burkholder 1992; Brobbel et al. 1996; Webb 1998; Dempson et al. 2002; Thorstad et al. 2003; Tsuboi and Morita 2004; Cooke and Suski 2005). Its importance is therefore likely to increase world-wide in most, if not all, recreational fisheries (Arlinghaus et al. 2007b). We present a positive outlook in that most hooking mortality estimates for European fish species or their relatives from the same genus reported so far were below 10%. It is important to realize that the average and median hooking mortality estimates in the present study were based on experimental studies published in the literature. Researchers might be inclined to induce a large gradient of treatments such that larger hooking mortality rates are estimated and reported than are likely to be induced under normal practical conditions. Because of this issue, one should not take the published average hooking mortality rates and uncritically assume they will occur in every recreational fishery. Instead, as many studies reviewed in the present paper have shown, hooking mortality rates can be very low in many situations and often approach zero (Pope and Wilde 2004; Pope et al. 2007; Thorstad et al. 2007). Nevertheless, there is further scope to keep hooking mortality low or even absent, and the findings of the present study can provide some useful directions. For example, managers and recreational anglers should be aware that water temperatures over a specific speciesdependent threshold will very likely lead to increased and unintended losses in released fish. Therefore, anglers are recommended to minimize effort under unfavorably high water temperature conditions when the intention is to release fish or the likelihood of catching undersize fish is high. Furthermore, the choice of terminal gear and bait should be considered with care; for example, for some species, avoidance of natural bait (especially in fishing for predators that are to be released) and possibly barbed hooks can help to improve the chance of survival of released fish after the release event. Consideration of these and other recent findings (Cooke and Suski 2005; Arlinghaus et al. 2007a,b) as well as adherence to recently published best practice guidelines in recreational fisheries (EIFAC 2008) can contribute to sustainable management of recreational fisheries and should be pursued further in close interaction with practitioners and anglers.

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