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Enhancing catch-and-release science with biotelemetry

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Abstract

Catch-and-release (C&R) angling is widely practised by anglers and is a common fisheries management strategy or is a by-product of harvest regulations. Accordingly, there is a growing body of research that examines not only the mortality associated with C&R, but also the sublethal physiological and behavioural consequences. Biotelemetry offers a powerful means of remotely monitoring the behaviour, physiology and mortality of fish caught and released in their natural environment, but we contend that its usefulness is still underappreciated by scholars and managers. In this study, we review the applications of biotelemetry in C&R science, identify novel research directions, opportunities and challenges. There are now about 250 C&R studies but only one quarter of these utilize biotelemetry. In fact, almost all of the C&R studies that have used biotelemetry have been conducted within the last decade. We found that the majority of C&R telemetry studies used either radio or acoustic telemetry, while comparatively few studies have used satellite technologies. Most C&R biotelemetry studies have been used to assess mortality rates, behavioural impairments or to evaluate the effects of displacement on fish. A small fraction of studies (<8%) have used physiological sensors despite the fact that these tools are highly applicable to understanding the multiple sublethal consequences of C&R and are useful for providing mechanistic insights into endpoints such as death. We conclude that C&R science has the potential to benefit greatly from biotelemetry technology, particularly with respect to providing more robust short-term and delayed mortality estimates and adopting a more integrative and comparative approach to understanding the lethal and sublethal impacts of C&R. However, there are still a number of challenges including (i) the need for appropriate controls and methodological approaches, (ii) the need for accounting for tagging and handling stress and mortality, and (iii) the need for certainty in assessing mortality. However, the benefits associated with C&R biotelemetry outweigh its disadvantages and limitations and thereby offer C&R researchers a suite of new tools to enhance fisheries management and conservation.

Keywords Angling, biotelemetry, catch-and-release, physiological telemetry, recreational fisheries, telemetry

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Introduction

The recreational fishing sector is considered to be a contributing factor to the decline of fish populations (Arlinghaus et al. 2002; McPhee et al. 2002; Post et al. 2002; Coleman et al. 2004; Cooke and Cowx 2004; Arlinghaus and Cooke 2005; Cooke and Cowx 2006). Multiple direct and indirect biological impacts are conceivable as a result of recreational exploitation of fish stocks (Lewin et al. 2006). Catch-and-release (C&R) angling is a conservation approach that is becoming an increasingly used practice by anglers, either through voluntary or mandated means as a by-product of harvest regulations (Cowx 2002: Cooke and Suski 2005: Arlinghaus et al. 2007). C&R has the potential to reduce the direct mortality associated with catchand-keep fisheries while conserving fish populations and maintaining the socioeconomic and cultural benefits of the recreational fishery (Policansky 2002; Lewin et al. 2006; Arlinghaus et al. 2007). However, C&R as a management approach is not without its limitations and can result in undesirable biological and ecological consequences (Cooke and Suski 2005; Arlinghaus et al. 2007).

The fundamental assumption of C&R is that released individuals will ultimately survive to contribute their genes to subsequent generations (Wydoski 1977; Cooke *et al.* 2002a). However, C&R can result in immediate, short-term or delayed mortality (reviewed in Muoneke and Childress 1994; Bartholomew and Bohnsack 2005). In addition, the capture, handling and release of fish is inherently stressful and is associated with a suite of sublethal consequences, including post-release behavioural impairments and physiological responses (Cooke et al. 2002a; Cooke and Sneddon 2007; Arlinghaus et al. 2007). At a global scale, recreational fisheries exploitation rates are estimated to be as high as 47.1 billion fish per annum, two-thirds of which are released (Cooke and Cowx 2004). With such a high proportion of fish being released by the recreational fishing sector, C&R research is becoming an increasingly important area of study, as managers demand robust scientific research to form the foundation of policy decisions and conservation efforts.

To address these concerns, the discipline of C&R science focuses on understanding the fundamental consequences of recreational fishing on the biology and survival of released fish, including outcomes at the community and ecosystem levels (Cooke and Schramm 2007). Biotelemetry is becoming increasingly popular among C&R researchers to study the sublethal (Cooke *et al.* 2002b) and lethal consequences of C&R angling (Pollock and Pine 2007). For the purpose of this study, the definition of biotelemetry includes the remote monitoring of

free-swimming fish in their natural environment (Cooke et al. 2004c) and also incorporates archival biologgers, which are devices that store data onboard for later downloading (Block 2005; Ropert-Coudert and Wilson 2005) or devices that initially store data and then later transmit data remotely, such as satellite transmitters (Block 2005). Although not a focus of this review, passive integrated transponder (PIT) tags can be used to identify individuals (Aalbers et al. 2004; Pope and Wilde 2004; Pope et al. 2007), allowing for the assessment of physical condition and mortality for recaptured fish and the determination of postrelease displacement and recapture rates. However, to our knowledge, PIT tags have only been used in an experimental C&R context to identify individual fish in pens, tanks or cages. For C&R science, biotelemetry facilitates the assessment of the behaviour, condition and fate (i.e. survival vs. mortality) of fish following release. Biotelemetry also enables the remote collection of physiological (Cooke et al. 2004a,b,c), behavioural (Nelson et al. 2005), energetic (Cooke et al. 2004a,c) and/or environmental data from free-living animals in their natural environments.

Despite its obvious advantages, biotelemetry is underused in contemporary C&R science. Accordingly, the purpose of this review is to provide an overview and synthesis of C&R biotelemetry. We highlight the applications and opportunities of this rapidly evolving field of study in the context of C&R. The first objective of this review is to describe the current state of C&R biotelemetry by providing a quantitative overview of the research that has been conducted to date. The second objective is to describe key applications of telemetry to understanding the biological consequences of C&R and discuss the opportunities and challenges of using biotelemetry to study C&R. This study presents the first quantitative review of the C&R biotelemetry literature, summarizes key studies and provides directions for future research. It is our hope that this article will facilitate greater use of biotelemetry in C&R research.

Traditional C&R research methods

Historically, field-based C&R science has been fraught with methodological challenges, as observing fish in the wild is inherently difficult and requires innovative approaches. Several methods have been used to understand the consequences of C&R, including external marking studies, holding pen/cage studies (Lucy and Arendt 2002; see Pollock and Pine 2007 for methodological discussion) and of late, biotelemetry. Traditional methods provide only minimal detail on the wide range of potential C&R consequences.

Confinement studies have been used as a costeffective means of monitoring post-release condition and survival (Muoneke and Childress 1994; Whoriskey et al. 2000; Duffy 2002; Lucy and Arendt 2002), but these approaches are generally unrealistic in a C&R context as they preclude an understanding of ecosystem interactions, such as post-release predation (Cooke and Philipp 2004; Thorstad et al. 2004), and do not allow for assessments of the fine-scale behavioural responses of free-swimming fish. Retention in pens and cages may also magnify injury, stress and mortality, potentially resulting in inaccurate assessments of mortality. In addition, confinement methods may not be practical for migratory species and/or species that require access to deep, open water, such as large pelagic fishes (Skomal 2007).

Mark-recapture studies can be useful for certain types of C&R research questions, including longterm data collection on survival rates (Pollock and Pine 2007), as this approach is cost-effective and enables studies to have a large sample size. However, there is uncertainty, even with model calculations, that C&R mortality estimates are accurate because of underreporting and naturally occurring mortality. This approach does not provide data on fine-scale movement behaviour which makes an assessment of behavioural impairments from C&R very difficult. This method does not easily allow researchers to link multiple endpoints associated with C&R, such as understanding the consequences of post-release behavioural impairments with respect to thermal habitat selection. While markrecapture studies provide very low resolution data on behaviour and mortality of a large sample size, telemetry studies provide high resolution data but generally on a smaller sample size. For mortality studies, it has been suggested by Pollock et al. (2004) that combining telemetry with markrecapture may help maximize sample size while maintaining the collection of high resolution data. Because of the challenges associated with traditional methods for studying C&R, a growing number of researchers are using biotelemetry. Biotelemetry enables fine-scale assessments of behaviour, mortality and other endpoints associated with C&R.

Quantitative overview of biotelemetry in C&R science

Arlinghaus et al. (2007) conducted a review of the C&R literature that had been published prior to August 2005. We updated this database using Web of Science, Google Scholar, Scholar's Portal and the American Fisheries Society search engine to survey the C&R literature that was published from September 2005 to May 2007. A number of search strings, including 'catch and release telemetry'. 'recreational fish telemetry', 'angling telemetry' and search techniques involving keywords, abstracts, full text and cited reference searches were used to maximize the number of records located. The search included peer-reviewed research articles, review articles that contained new data, graduate theses and government reports. All searching, summaries and analyses were conducted by the same researcher to ensure consistency.

In total, dating to 1957, 242 C&R studies were found, 55 (23%) of which used biotelemetry (Table 1). The publication rate (assumed to be reflective of actual research patterns) for C&R and biotelemetry studies has increased over time, with a marked increase in recent years. For example, 73% of all C&R biotelemetry studies have been published since 2000 (Fig. 1). Of these, 70% of studies were conducted on freshwater species and 30% on marine species. This temporal trend reflects recent advancements and potentially increased affordability/awareness of telemetry technology, along with smaller size, improvements in onboard sensor technology and improved battery life (Cooke et al. 2004c). Also, fish biologists may be increasingly applying techniques that have been traditionally used in behavioural ecology to more applied research questions.

A number of biotelemetry technologies are available and have been described previously in a C&R context (Cooke *et al.* 2002a; Skomal 2007). In the C&R literature, most studies have used radio (40%) or acoustic (44%) transmitters. Less common technologies include electromyogram (EMG) transmitters (7%), pop-up satellite archival tags (PSATs; 9%) and combined acoustic and radio tags (CART; 2%; Table 2). Transmitters are most commonly surgically implanted or externally attached, while gastric tagging is less common but is useful in certain

contexts (e.g. anadromous migrating salmonids that are not feeding; Table 3). External attachment methods include attaching a 'backpack transmitter' that can be secured by using wires that are fed through the dorsal musculature and wound together against a backing plate to minimize scale loss and tissue damage. The attachment procedure is rapid, noninvasive and does not require fish to be anaesthetized. However, depending on the ratio of fish size to transmitter size, as well as transmitter design, colour and shape, there is potential for the backpack to increase drag and make the fish appear more conspicuous. Other external approaches have included a transmitter and float assembly (Osborne and Bettoli 1995). The assembly can be attached to a steel dart or pin which is then inserted through the dorsal musculature. If the assembly is attached using dissolvable suture material (e.g. polyglactin), it will dissolve within 3-4 weeks, which reduces the burden of the device on the fish and allows the transmitter to be recovered. As a cost-effective measure, inexpensive thermal loggers can be securely fastened to the transmitter and retrieved from the float assembly and downloaded to obtain thermal histories for individual fish. Recovery also allows for the refurbishment and redeployment of old transmitters by replacing batteries. PSATs are becoming an increasingly used technology in marine environments. Twenty-nine per cent of reviewed marine C&R biotelemetry studies used PSATs (Table 2). PSATs are attached externally, usually via dart, log data and are then jettisoned from fish. The stored data are then transmitted by satellite link (reviewed in Brill and Lutcavage 2001). CART transmitters have only been used once in the C&R biotelemetry literature (Young and Isley 2006). The advantages and limitations of using these different technologies are summarized in Table 4.

Over 75% of C&R biotelemetry studies have occurred in North America (n = 42; 76% freshwater; 24% marine). Proportionally, freshwater studies tended to favour radio transmitters (55%) while acoustic/ultrasonic transmitters were used most often in marine environments (71%; Table 2). Species from the families Centrarchidae (27%) and Salmonidae (24%) were the most commonly studied freshwater species and Istiophoridae (15%) and Scombridae (11%) were the most commonly studied marine species (Table 3). Few studies have integrated multiple endpoints associated with C&R (6%). Overall, behaviour (73%), mortality (69%) and assess-

Table 1 Complete list of all catch-and-release (C&R) biotelemetry studies (N = 55), ordered by year of publication. The biotelemetry technology used included acoustic, radio, combined acoustic and radio (CART), pop-up satellite tags (PSAT), and several physiological telemetry devices including electromyogram (EMG) and heart rate.

_	Bafaranca	Snacias	2	Technology	Attachment	Besearch ohiective	Study type
			-	6800-000			odki konio
	Jolley and Irby (1979)	Atlantic sailfish (Istiophorus platy-	8	Acoustic	Internal	Assessment of injury and short-term	Descriptive
		<i>pterus,</i> Istiophoridae)				mortality following tagging and release	
	Lough (1979)	Steelhead trout (<i>Oncorhynchus</i> <i>mvkiss</i> Salmonidae)	9	Radio	Gastric	Evaluation of live-capture methods and identification of specific stocks and	Descriptive
						respective rates of movement	
	Margeneau (1987)	Northern pike (<i>Esox luciu</i> s, Esocidae)	ი	Radio	Internal	Assessment of angling vulnerability based on known locations	Descriptive
	Block <i>et al.</i> (1992)	Blue marlin (<i>Makaira nigricans</i> ,	9	Acoustic	External	Assessment of post-release swimming	Descriptive
		Istiophoridae)				speeds, depth and temperature prefer- ences	
	Bendock and Alexandersdottir (1993)	Chinook salmon (<i>O. tshawytscha</i> , Salmonidae)	446	Radio	External	Assessment of injury and short-term post-release mortality	Descriptive
	Osborne and Bettoli (1995)	Striped bass (Moronoe saxatilis, Moronidae)	105	Acoustic	External	Validation of a technique for attaching retrievable ultrasonic transmitters for C&R research	Descriptive
	Lee and Bergerson (1998)	Lake trout (<i>Salvelinus namaycush</i> , Salmonidae)	25	Acoustic	External	Assessment of the influence of thermal and oxygen stratification on post-release mortality	Descriptive
	Ridgway and Shuter (1996)	Smallmouth bass (<i>Micropterus dolomieu</i> , Centrarchidae)	18	Acoustic	Internal	Assessment of post-release displacement	Comparativ
	Stang <i>et al.</i> (1996)	Largemouth bass (<i>Micropterus</i> salmoides, Centrarchidae), smallmouth bass	42	Radio	External	Assessment of post-release displace- ment from tournaments	Comparativ
	Anderson <i>et al.</i> (1998)	Atlantic salmon (<i>Salmo salar</i> , Sal- monidae)	10	Heart rate telemetry	Internal	Assessment of post-release cardiac function	Integrative
	Bettoli and Osborne (1998)	Striped bass	98	Acoustic	External	Assessment of hooking mortality and	Comparative

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						Attachment		
	2	Reference	Species	Ľ	Technology	method	Research objective	Study type
	12	Edwards (1998)	Tarpon (<i>Megalops atlanticus</i> , Megalopidae)	ω	Acoustic	Internal	Assessment of post-release behaviour and fate	Descriptive
	13	Webb (1998)	Atlantic salmon	25	Acoustic	Gastric	Assessment of post-release behaviour and fate for migratory	Descriptive
							species	
	14	Pepperell and Davis (1999)	Black marlin (<i>Makaira indica,</i> Istiophoridae)	ø	Acoustic	External	Assessment of the behavioural consequences of C&R	Descriptive
Jour	15	Bettoli <i>et al.</i> (2000)	Sauger (<i>Sauger canadensis</i> , Percidae)	19	Radio	External	Assessment of survival from hook- ing injuries	Comparative
nal co	16	Cooke <i>et al.</i> (2000)	Largemouth bass	10	EMG	Internal	Assessment of the consequences	Integrative
mpil							ט כמו טו אמיפוגמ כמים טפוומע- iours	
atio	17	Mäkinen <i>et al.</i> (2000)	Atlantic salmon	25	Radio	Internal	Comparison of gear types	Comparative
n ©	18	Richardson-Heft <i>et al.</i> (2000)	Largemouth bass	82	Radio	Internal	Assessment of the consequences	Comparative
200							of C&R on movement at a C&R	
08							tournament	
Bla	19	Ridgway (2000)	Largemouth bass	18	Radio and acoustic	Internal	Evaluation of movements, home	Comparative
ckw	ç			ac		locator l	range and survival	Decerictive
ell P	Ŋ	WINNISKEY EL al. (2000)	Auguro Samon	07	naulo		Assessment of the benavioural consequences of C&B	nescriptive
ublis	21	Hightower <i>et al.</i> (2001)	Striped bass	51	Acoustic	Internal	Comparison of fishing and natural	Comparative
shir							mortality rates	
ng Ltd,	22	Arendt and Lucy (2002)	Tautog (<i>Tautoga onitis</i> , Labridae)	33	Acoustic	Internal	Evaluation of immediate survival rates from C&R	Descriptive
FI	23	Brill <i>et al.</i> (2002a)	Bluefin tuna (<i>Thunnus thynnus</i> ,	5	Acoustic	External	Evaluation of the consequences of	Descriptive
SH			Scrombridae)				C&R on behaviour and physiol-	
and							ogy	
l FI	24	Brill <i>et al.</i> (2002b)	Bluefin tuna	5	Acoustic	External	Assessment of post-release	Descriptive
© SHI							horizontal and vertical move-	
20 E R							ments	
08 Tł IES,	25	Bunt <i>et al.</i> (2002)	Smallmouth bass	18	Radio	Internal	Characterizing the mobility of tournament caught fish in a	Descriptive
ne Au 9, 79							riverine system	
thors 105								

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Table 1 Continued.

z	Reference	Species	ч	Technology	Attachment method	Research objective	Study typ
26	Cooke <i>et al.</i> (2002b)	Largemouth bass, smallmouth bass	33	EMG	Internal	Assessment of the physiological consequences of C&R using EMG transmittars	Compar
27	Graves <i>et al.</i> (2002)	Blue marlin	6	PSAT	External	Evaluation of post-release survival rates	Descrip
28	Pearson (2002)	Largemouth bass	13	Acoustic	Internal	Evaluation of the movement patterns of displaced fish	Compai
50	Skomal and Chase (2002)	Blue shark (<i>Prionace glauca</i> , Carcharhinade), yellowfin tuna (<i>Thunnus albacares</i> , Scombri- dae), white marlin (<i>Tetrapturus albidus</i> , Istiophori- dae), bluefin tuna	15	Acoustic	External	Assessment of the physiological effects of C&R in relation to post-release survivorship	Integrat
30	Stuby (2002)	Coho salmon (<i>Oncorhynchus kisutch</i> , Salmonidae)	99	Radio	Gastric	Evaluation of the consequences of C&R across a range of geographical locations	Descrip
31	Aguilar (2003)	Red drum (<i>Sciaenops ocellatus</i> , Sciaenidae)	52	Acoustic	External	Assessment of hooking mortality and behavioural alterations from C&R	Descrip
32	Domeier <i>et al.</i> (2003)	Striped marlin (<i>Tetrapturus audax</i> , Istiophoridae)	80	PSAT	External	Assessment of mortality from different gear types	Compa
33	Lowerre-Barbieri <i>et al.</i> (2003)	Common snook (<i>Centropomus andersonii</i> , Centropomidae)	5	Acoustic	Internal	Understanding the consequences of C&R on reproductive output	Descrip
34	Thorstad <i>et al.</i> (2003)	Atlantic salmon	30	Radio	External	Understanding the consequences of C&R on spawning fish	Descrip
35	Cooke and Philipp (2004)	Bonefish (<i>Albula vulpes</i> , Albulidae)	35	Acoustic	Gastric	Understanding the consequences of C&R on behaviour and mortality (including predation)	Descrip
36	Cooke <i>et al.</i> (2004b)	Largemouth bass	7	Heart rate telemetry	Internal	Assessment of the consequences	Integra

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I						Attachment		
-	z	Reference	Species	c	Technology	method	Research objective	Study type
37	~	Gurshin and Szedlmayer (2004)	Sharpnose shark (<i>Rhizoprionodon terraenovae</i> , Carcharhinidae)	0	Acoustic	External	Assessment of the short-term sur- vival and movement following C&R	Descriptive
38	œ	Thorstad <i>et al.</i> (2004)	Nembwe (<i>Serranochromis</i> robustus, Cichlidae), threespot tilapia (<i>Oreochromis</i> andersonii, Cichlidae)	24	Radio	External	Evaluation of the effects of C&R on large African cichlids	Descriptive
39	¢	Westover and Heidt (2004)	Bull trout (<i>Salvelinus confluentus</i> , Carcharhinidae)	71	Radio	Internal	Examination of post-release behaviour and survival	Descriptive
40	0	Young and Isley (2004)	Striped bass	48	Radio	Internal	Quantification of temporal and spa- tial estimates of mortality	Descriptive
41	_	Beittinger <i>et al.</i> (2005)	Striped bass	59	Acoustic	External	Assessment of hooking mortality and physiological condition in relation to live-release tube con- finement	Integrative
42	0	Faler <i>et al.</i> (2005)	Bull trout	25	Radio	Internal	Assessment of post-release behaviour and survival	Descriptive
43	~	Horodysky and Graves (2005)	White marlin	41	PSAT	External	Characterization of survival and initiary based on hook type	Comparative
44	4	Kaintz and Bettoli (2004)	Smallmouth bass	54	Acoustic	External	Assessment of mortality and behaviour of tournament-caught fish	Descriptive
45	10	Nelson <i>et al.</i> (2005)	Steelhead	226	Radio	Gastric	Evaluation of behaviour and sur- vival of wild and hatchery fish following C&R	Comparative
46	6	Waters <i>et al.</i> (2005)	Largemouth bass	44	Acoustic	Internal	Evaluation of behavioural and sur- vival following C&R	Descriptive
6 © 200	2	Skomal (2006)	Blue shark, yellowfin tuna, white marlin, bluefin tuna	52	PSAT	External	Assessment of the physiological and the phys	Integrative
8 8 The	~	Young and Isley (2006)	Striped bass	30	CART	Internal	Assessment of C&R tournament survival and behaviour	Descriptive
약 Authors	¢	Danylchuk <i>et al. (2</i> 007a)	Bonefish	12	Acoustic	Gastric	Comparison of handling methods on survival and behaviour	Comparative

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Table 1 Continued.

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:		-			Attachment	:	i
z	Reference	Species	u	Technology	method	Research objective	Study type
50	Gravel and Cooke (2008)	Smallmouth bass	63	Radio	External	Evaluation of the consequences of	Integrative
						barotrauma on physiology, behaviour and fate at a tourna-	
						ment	
51	Horodysky <i>et al.</i> (2008)	White marlin	47	PSAT	External	Comparison of gear types on phys- iology and behaviour	Comparative
52	Klefoth (2007)	Northern pike	72	Radio	Internal/external	Evaluation of physiological and	Integrative
						behavioural consequences of	
						C&R	
53	Klefoth <i>et al.</i> (2008)	Northern pike	20	Radio	Internal	Assessment of the short-term	Comparative
						effects on behaviour and habitat	
						choice	
54	Thompson (2007)	Largemouth bass	58	Radio	External	Assessment of the consequences	Integrative
						of air exposure and water tem-	
						perature on physiology and	
						behaviour	
55	Thorstad <i>et al.</i> (2007)	Atlantic salmon	44	Radio	External	Assessment of the consequences	Descriptive
						of C&R on spawning migration	

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Figure 1 Number of catch-and-release (C&R) biotelemetry studies by year.

ments of injury, gear and handling effects (35%) were the most common endpoints measured (Table 3).

Applications of biotelemetry to C&R science

Mortality studies

Despite improved knowledge of the factors that contribute to mortality, delayed mortality from C&R is still high and has been recorded at nearly 90% for some marine and freshwater species (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005). Consequently, many knowledge gaps still exist. Reducing the uncertainty surrounding mortality rates is necessary for the effective management of C&R fisheries. Biotelemetry can be used to estimate mortality rates and can also be linked with other techniques to gain insight into the factors that contribute to mortality. Taken together, this information is required to improve the management and conservation of fish populations. However, biotelemetry alone cannot eliminate the uncertainty of the consequences of C&R. Accordingly, we present several case studies below where biotelemetry has been used to assess mortality in a C&R context. Within, we highlight the limitations and challenges of this approach.

Mortality is generally categorized as immediate, short term or long term. Immediate mortality is measured when a fish is dead upon landing or dies prior to or during release (Pepperell and Davis 1999). Short-term mortality may be observed within 24-48 h of an angling event, often as a result of hooking injuries in tissue or organs that result in severe blood loss immediately following release (Muoneke and Childress 1994) or elevated predation rates due to the physiological and/or behavioural impairments resulting from release (Cooke and Philipp 2004). However, delayed mortality from C&R is often defined as mortality that occurs more than 72 h following the angling event (Pollock and Pine 2007). Consequently, delayed mortality is difficult to quantify and there is a high degree of uncertainty in determining mortality rates in a C&R context. Biotelemetry is often used as a means of reducing this uncertainty. In fact, nearly 80% of the studies reviewed here used C&R telemetry to quantify mortality (Table 3).

Determining with certainty when, or even if, a mortality event has occurred can be difficult, even with the use of biotelemetry. Transmitters with mortality sensors can be very effective at determining mortality (Eiler 1990), but the high cost of transmit-

Table 2 Number of catch-and-release angling studies that have used different transmitter types and attachment methods in freshwater and marine environments. Note that this table includes one freshwater study that used both radio and acoustic transmitters (i.e. Ridgway 2000), N/A; not applicable.

	Freshwat	ter		Marine			Total		
Transmitter type	Internal	External	Gastric	Internal	External	Gastric	Internal	External	Gastric
Radio	9	9	4	0	0	0	9	9	4
Acoustic/ultrasonic	6	6	0	2	7	3	8	13	3
Combined acoustic and radio	1	0	0	0	0	0	1	0	0
Pop-up satellite	N/A	0	N/A	N/A	5	N/A	N/A	5	N/A
Activity/heart rate/electromyogram	4	0	N/A	0	0	N/A	4	0	N/A
Total	20	15	4	2	12	3	22	27	7

© 2008 The Authors Journal compilation © 2008 Blackwell Publishing Ltd, FISH and FISHERIES, 9, 79–105 **Table 3** Catch-and-release (C&R) endpoints that have been examined in studies that have used biotelemetry (by family). Studies with multiple endpoints and studies on more than one species or family of fish are recorded in the table. Note that although data are extracted from 55 studies, several studies included multiple species and endpoints.

		C&R end	points						
Family	Species	Mortality	Injury	Stress	Behaviour	Spawning or migration	Fitness	Gear or handling	Ecosystem interactions
Centrarchidae	Largemouth bass, smallmouth bass	6	2	4	11	1	1	2	0
Salmonidae	Atlantic salmon, bull trout chinook salmon, coho salmon, lake trout, steelhead trout	9	2	1	9	7	5	2	0
Istiophoridae	Black marlin, blue marlin, white marlin, striped marlin, Atlantic sailfish	5	3	2	5	0	0	1	0
Moronidae	Striped bass	6	1	1	2	0	0	2	0
Scombridae	Bluefin tuna, yellowfin tuna	4	0	2	4	0	0	0	0
Albulidae	Bonefish	3	0	0	3	0	0	1	1
Carcharhinidae	Blue shark, Atlantic sharpnose shark	3	0	2	3	0	0	0	0
Cichlidae	Nembwe, threespot tilapia	1	0	0	1	0	1	0	0
Centropomidae	Common snook	0	0	0	1	1	1	0	0
Esocidae	Northern pike	2	1	1	2	0	0	2	0
Labridae	Tautog	1	0	0	1	0	0	0	0
Percidae	Sauger	1	1	0	0	0	0	0	0
Sciaenidae	Red drum	1	0	0	1	0	0	1	0
Megalopidae	Tarpon	1	0	0	1	0	0	1	0
	Total	43	10	13	44	9	8	12	1

ters with sensor technology can preclude their use. As a consequence, the majority of C&R biotelemetry studies determine mortality based on the duration of fish immobility. There are obvious flaws in this approach, as spurious conclusions can be drawn from fish that are immobile for a long period of time but may remain alive. Therefore, it is recommended that other techniques be combined with biotelemetry to further reduce the uncertainty of mortality rates. For example, if a potential mortality is identified using biotelemetry, SCUBA, snorkelling or underwater video can be used in many systems to conclusively determine fate and spurious assessments of mortality. Alternatively, there is a need for more reliable and cost-effective mortality sensors that can be incorporated into biotelemetry devices.

Direct mortality studies

Biotelemetry has been used to link mortality with hooking injury (Bendock and Alexandersdottir

1993; Bettoli et al. 2000). As with any C&R and biotelemetry study, it is difficult to exclusively attribute mortality to only the C&R event. A multitude of other factors may contribute to mortality, including tagging-related effects and naturally occurring (i.e. independent of the angling event) mortality. For example, Bendock and Alexandersdottir (1993) found that hooking mortality was under 8% for 446 migrating Chinook salmon (Oncorhynchus tshawytscha, Salmonidae) that were caught and released in a 3-year study on the Kenai River, Alaska. Although survival rates were relatively high in this study, mortality may have in fact been overestimated as natural mortality is often linked with difficult spawning migration of this species (Hightower et al. 2001). An alternative method would be to tag a large number of fish and recapture a random fraction of these to obtain appropriate control fish (see Klefoth et al. 2008). In closed systems with zero fishing pressure, it is possible to use telemetry to determine natural rates

Factor	External ('back pack')	External (dart)	Gastric	Internal
Drag and fouling	Device and harness package causes increased drag and can promote fouling leading to potential overestimates of mortal- ity and behavioural impacts of C&R	Device and harness package causes increased drag and can promote fouling leading to potential overesti- mates of mortality and behavioural impacts of C&R. Tend to be conspic- uous and may attract predators, par- ticularly in marine environments were	Trailing antennas from radio tags can cause drag and lead to fouling	Trailing antennas from radio tags can cause drag and lead to fouling
Tag loss or shedding	Short- to medium-term retention (days to weeks)	uaris are otten used Short- to long-term retention (days to months)	Regurgitation can occur; regarded as a short-term attachment technique	Typically long-term retention (years)
Skill level and expertise	Simple attachment procedure; limited training and expertise	Simple attachment procedure; limited training and expertise	(uays to weeks) Simple attachment procedure; limited training and expertise	Complicated attachment procedure; requires specialized training, exper-
Speed of procedure Need for anaesthesia	Rapid procedure (seconds to several minutes) Not essential, although preferred; useful for calming fish to make procedure easier. May be required by animal welfare committee. Anaesthesia can alter behaviour and poten- tially confound C&R studies	Very rapid procedure (seconds) Rarely used, particularly for satellite tags. Darts can be easily applied to marine pelagics without bringing them aboard a vessel	Very rapid procedure (seconds) Not essential, although preferred; use- ful for calming fish to make proce- dure easier. May be required by animal welfare committee. Anaesthe- sia can alter behaviour and poten- tially confound C&R studies	Longest procedure; requires 3–10 min Essential in almost all instances; needed to immobilize fish and to minimize sensory capacity during potentially painful procedures. Need for anaesthesia and surgery reduces the utility of this technique for C&R
Ease of field use	Easy field use	Easy field use	Easy field use	research Requires specialized equipment; can be carried out in field settings with appropriate gear
Species limitations	Not well suited to small fish, migratory species, fish living in highly vegetated or fast-water habitate	Typically limited to larger species, often in marine environments	Limited to fish that are not actively feeding	Some species are known to expel tags
Potential for behaviour- al alteration	Possible from drag or attempts by the fish to rub off device; may attract predators	Possible from drag or attempts by the fish to rub off device; may attract predators	Minimal in non-feeding fishes or pro- vided rapid expulsion prior to prob- lems with feeding/nutrition	Minimal following healing and assum- ing device is not too big (mass or volume, or length of antenna). How- ever, the need for anaesthesia and a lengthy surgical procedure may in- crease potential for behavioural alter- ations

Table 4 Summary of tagging methods for biotelemetry and biologging devices and their advantages and disadvantages for catch-and-release (C&R) studies.

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Factor	External ('back pack')	External (dart)	Gastric	Internal
Type of C&R studies	Well suited to assessments of short term and delayed (up to several weeks or months) mortality. Useful for behavioural assess- ments. Can be combined with non-lethal physiological biopsies	Well suited to assessments of short term and delayed (up to several weeks) mortality. Useful for behavio- ural assessments. Can be combined with non-lethal physiological biopsies	Well suited to short term (up to several weeks or months) assessments of mortality and behaviour. Can be combined with non-lethal physiological biopsies	Useful for long-term assessments of mortality. Not optimal for short-term behavioural assessments. Can be combined with non-lethal physiologi- cal biopsies. The preferred technique for physiological telemetry studies (e.g. heart rate and activity) as most sensor electrodes must be placed internally

Table 4 Continued.

of mortality and contrasting these baseline rates to values from angling-induced mortality (Hightower *et al.* 2001; Waters *et al.* 2005). However, this is difficult in open systems because of emigration or removal from fisheries (Pollock and Pine 2007). Mortality from transmitter implantation is another potential factor that may spuriously elevate mortality rates (see 'Challenges' section below). Transmitter failure can also lead to overestimates of angler harvest.

Telemetry can be used to understand the direct and indirect factors that contribute to mortality. These factors often include environmental variables (e.g. temperature) and characteristics of the angling event (e.g. handling type, air exposure duration, gear-types). For example, Lee and Bergerson (1996) used radio telemetry to evaluate the influence of thermal and oxygen stratification on the mortality of large (>56 cm) lake trout (Salvelinus namaucush. Salmonidae) in Lake Granby, Colorado. These authors found that thermal refuge locations (sites where water temperatures were <12 °C) contained low dissolved oxygen (3 mg L^{-1}) during 2 months in late summer. When the oxygen conditions were poor, mortality approached 88% for fish that were angled and released compared to other times of the year when mortality was less than 12% due to the availability of thermal refugia. Bettoli and Osborne (1998) found that mortality rates of angled striped bass (Morone saxatilis, Moronidae) were linearly related to air temperature, but not angling variables such as landing and handling duration, bait type, fish length or water temperature. Radio telemetry results revealed that surviving fish remained in warm surface waters for approximately 2 h following release and then descended into cooler and deeper waters, while fish that did not survive surfaced with 1.5 h due to barotrauma. This approach has also been applied in the context of marine pelagic fish. Domeier et al. (2003) used PSATs to assess the post-release survival, movement, distribution and associations with temperature and depth of striped marlin (Tetrapturus audax, Istiophoriade). The study quantified the mortality associated with I-style hooks vs. circle hooks, finding that circle hooks reduced bleeding and injury. The authors used PSAT temperature and depth data to assess mortality rates and found that mortality was high (26%), occurring within 5 days post-release.

Pollock and Pine (2007) recently described a number of general approaches for the design and

analysis of biotelemetry studies to assess C&R mortality, including strategies for the accurate estimate of short-term and long-term C&R mortality, contrasting containment vs. telemetry studies and assessments of population-level impacts of C&R mortality. The authors concluded that in a C&R context, biotelemetry is a useful tool for understanding mortality and the factors that contribute to mortality.

Indirect mortality studies

Biotelemetry has been used to document predation rates of fish that are caught and released, which is often linked with behavioural impairments, such as reduced fleeing potential. Following release, predation rates can be quite high, as released fish may be physiologically stressed and unable to escape from predators. This is particularly salient in marine systems where predator burdens are high but can also occur in freshwater environments from birds (Thorstad et al. 2004). In a number of studies, assessments of predator-prey interactions have not been the primary focus of the study and have instead been coincidentally documented on a small subset of tagged individuals (Jolley and Irby 1979; Block et al. 1992; Edwards 1998; Pepperell and Davis 1999; Thorstad et al. 2004; Danylchuk et al. 2007a).

Given this observational evidence it is likely that appropriately designed biotelemetry studies with larger sample sizes would document significant post-release mortality as a result of predation in systems with high predator burden. For example, Cooke and Philipp (2004) found that in an area of high shark abundance, all predation, which accounted for 39% of the total number of bonefish (Albula vulpes, Albulidae) occurred within 30 min of release. In areas of low shark abundance, no predation was observed. Mortality was associated with equilibrium loss and periods of approximately 30 min of immobility following the angling event. More research that specifically addresses the issue of post-release predation is required to gain a better understanding of the relative survival rates of caught-and-released fish with respect to predation.

C&R biotelemetry studies on physical condition and physiology

In a C&R context, fish capture generally involves hooking, netting and physical handling coupled with high anaerobic activity and air exposure. These stimuli disrupt homeostasis and elicit a physiological stress response (reviewed in Arlinghaus et al. 2007; Skomal 2007). Although the stress response is considered to be adaptive, it can result in sublethal physiological and/or behavioural impairments, or in extreme cases can lead to mortality (Arlinghaus et al. 2007). Sublethal endpoints generally include indicators of physical trauma, physiological stress, behavioural impairments, and a series of other indicators of sublethal impairments. Other sublethal indicators can include disease and pathological changes (Steeger et al. 1994: Borucinska et al. 2002), reproductive impairments (Cooke et al. 2000) and reduced growth/ energetics (Clapp and Clark 1989). In combination with a variety of techniques described below, biotelemetry is a powerful tool to assess these sublethal impacts of C&R.

Physiological telemetry permits the remote monitoring of physiological and behavioural variables simultaneously. Previously, these measures could only be obtained in the laboratory. Despite the utility of this technology, few C&R studies have used physiological telemetry. In fact, only two C&R studies have used heart rate telemetry (Anderson et al. 1998: Cooke et al. 2004b) and two studies have used EMG telemetry (Cooke et al. 2000, 2002b). Heart rate telemetry involves the placement of electrodes adjacent to the pericardial cavity to detect heart beat activity (Cooke et al. 2004a). Anderson et al. (1998) used heart rate telemetry to assess the increase in heart rate and recovery of C&R on Atlantic salmon (Salmo salar, Salmonidae). The authors found that post-angling heart rate increased by 15-20% across a range of temperature groups following angling. Recovery occurred within 16 h of release. Cooke et al. (2004b) took a similar approach by using heart rate telemetry to assess angling-induced cardiac disturbance in free-swimming largemouth bass (Micropterus salmoides, Centrarchidae). This application of heart rate telemetry allows for the reliable quantification of remote postexercise physiological activity and recovery. Cardiac output studies can provide a correlate of oxygen consumption by incorporating heart rate and stroke volume data. Unfortunately, cardiac output studies are limited to the laboratory as remote technology is not currently available to monitor cardiac output in fish (Cooke et al. 2002a).

Electromyogram telemetry provides measurement of locomotory activity and energetics of freeswimming fish. To date the only C&R EMG telemetry study has been conducted on centrarchids. Cooke et al. (2000) found that largemouth bass that were angled from their nests had impaired locomotory activity 24 h after angling compared to non-nesting males that recovered within 2 h post-release. The authors concluded that the reduced activity of nesting fish following C&R, combined with the increased predation rates of brood predators due to the short-term removal of the nest-guarding males, increases the likelihood of nest abandonment and reduces fitness. Cooke et al. (2002b) used EMG telemetry to study the crowding stress of smallmouth bass (Micropterus dolomieu, Centrarchidae) associated with livewell confinement. The authors found that when fish were held alone or with one other individual, a brief period of high activity was observed followed by low activity. When fish were introduced into livewells at densities of four or six fish, they showed heightened and variable activity during the entire retention period. Further information on C&R and physiological telemetry can be found in two syntheses by Cooke et al. (2002a, 2004a).

The sublethal consequences of C&R can be understood by combining behavioural data obtained from biotelemetry with other relevant sublethal endpoints, such as indicators of physiological stress. Physiological indices (e.g. stress, osmoregulatory status) can be obtained non-lethally from blood samples collected from angled fish in the wild to understand fish condition. These measures can be used as correlates of post-release mortality (Skomal 2007). Integrative studies that often combine multiple sublethal endpoints are described in more detail in the section 'Integrative C&R studies using biotelemetry', below.

Behavioural telemetry and C&R

Changes in movement following C&R

Behavioural changes following C&R include changes in swimming behaviour (Pepperell and Davis 1999; Klefoth *et al.* 2008), habitat associations (Horodysky *et al.* 2008; Klefoth *et al.* 2008) and reproductive and migratory behaviours (Cooke *et al.* 2000; Thorstad *et al.* 2003, 2007; Hanson *et al.* 2007). Biotelemetry can be used to assess behavioural impairments from C&R. For example, Pepperell and Davis (1999) used acoustic telemetry to describe the post-release activity patterns, temperature associations, and diel vertical and horizontal migrations of black marlin (*Makaira indica*, Istiophoridae) off the Great Barrier Reef, Australia. Released fish rarely moved below the thermocline and maintained temperatures of 8°C below surface water temperatures. Similar studies have been conducted on white marlin (*Tetrapturus albidus*, Istiophoriade) (Horodysky and Graves 2005) and blue marlin (*Makaira nigricans*, Istiophoridae) (Graves *et al.* 2002) using PSATs.

Along with assessments of movement, biotelemetry can be used to assess post-release habitat associations. Horodysky et al. (2008) used PSATs to assess habitat utilization and vertical movements of white marlin that were caught and released on either commercial or recreational fishing gear. The authors found that released fish associated with surface waters less than 10 m deep and displayed characteristic vertical excursions from surface to depths averaging 51 m similar to those described by Pepperell and Davis (1999). Vertical descents followed either a distinctly v-shaped or u-shaped pattern. Similar descriptive behavioural studies have been conducted on various freshwater species (Young and Isley 2004; Thompson 2007; Klefoth et al. 2008).

C&R tournaments and displacement

A number of studies have focused on the behaviour and survival of fish caught in live-release angling tournaments (Siepker et al. 2007). Live release fishing tournaments have been linked with mortality (Furimsky et al. 2003; Killen et al. 2003; Edwards et al. 2004), physiological stress (Suski et al. 2004), behavioural alterations (Young and Isley 2006) and barotrauma (Gravel and Cooke 2008). During tournament weigh-ins, fish are often displaced several kilometres from their initial capture locations. Biotelemetry studies have assessed post-release behaviour, the time to return to initial capture sites and overall success of returning to initial capture locations. The majority of these studies have focused on black bass tournaments (e.g. Stang et al. 1996; Richardson-Heft et al. 2000; Bunt et al. 2002; Pearson et al. 2002). The question of whether or not displaced fish subsequently return to initial capture locations allows for an understanding of whether or not live-release tournaments have negative consequences on post-release behaviour and fish distributions. Traditional approaches have included mark-recapture studies to assess displacement and return rates (see Traditional C&R research methods, above). Biotelemetry allows for accurate assessments of fish movement and behaviour following release and allows for the quantification of return rates. For example, seasonal differences in return rates were observed for largemouth bass that were displaced 15-21 km in Chesapeake Bay. Fish released in spring tended to return within 3 months compared to fish that were released in autumn that took more than twice that time to return (Richardson-Heft et al. 2000: Wilde 2003). However, post-release movement is often unpredictable, which can result in challenges with tracking fish locations. As a consequence, movement zones are often developed in order to gauge movement and behaviour patterns (Gravel and Cooke 2008); however, this approach must be implemented objectively in order to reduce bias.

Beittinger et al. (2005) used biotelemetry to quantify the effects of hooking injury on striped bass in Lake Murray, South Carolina. Recently, the U.S. National Striped Bass Association endorsed live-release tubes, which are cylindrical recovery tanks with recirculating water, to promote survival of released striped bass, particularly at tournaments. These authors used telemetry to record behaviour and mortality and assessed the stress physiology associated with C&R angling for a subset of fish by looking at post-capture concentrations of plasma cortisol, glucose, lactate, and osmolality to assess angling stress and subsequent holding in live-release tubes. Although this study did not specifically integrate physiological and behavioural endpoints, the notion of pairing physiological condition with post-release behaviour is relevant to understanding the shortterm consequences of C&R (see Integrative C&R studies using biotelemetry, below). The authors observed zero mortality during cool water temperatures in spring, but the overall mortality rate during summer was 83%. Plasma cortisol, glucose, lactate and osmolality were positively related to live-release tube residence time and recovery of these indicators began after 150 min. Young and Isley (2006) conducted a telemetry study to assess the post-release dispersal behaviour and survival of striped bass from tournament weigh-in sites. The authors found that hooking, holding, displacement and weigh-in did not adversely affect long-term behaviour.

An integrative study by Gravel and Cooke (2008) examined the physiological and behavioural

consequences of tournament-caught smallmouth bass in relation to barotruama. Barotrauma occurs primarily in physoclistous species, where the swim bladder does not connect directly to the digestive tract, when fish are rapidly displaced from deep water to shallow water. Barotrauma can lead to haemorrhaging, tissue damage and swim bladder overinflation, which can lead to sublethal consequences (Hannah and Matteson 2007). Gravel and Cooke (2008) integrated both biosampling and biotelemetry techniques to link the pre-release physiological status and post-release behaviour and fate in relation to barotrauma. Non-lethal blood samples were collected to assess whole-blood concentrations of lactate and glucose and radio transmitters were externally attached to monitor post-release behaviour and fate. The concept of linking behaviour, physiology, and fate with biosampling and biotelemetry is novel for the study of the consequences of C&R angling, but similar methods have been used in other areas of fisheries research. For example, comparable approaches have been used to understand the factors contributing to migration failure in Pacific salmonids caught in commercial purse seines (Cooke et al. 2005a) and to assess the fate of blue shark (Prionace glauca, Carcharhinidae) released as commercial longline bycatch (Moyes et al. 2006). Gravel and Cooke (in press) found that blood lactate and glucose concentrations were elevated in fish exhibiting signs of barotruama, and were highest in fish that died. Biotelemetry revealed that over 20% of the fish that showed signs of barotrauma died, while an additional 25% were moribund within 5-6 days following release. All fish that did not show signs of barotrauma survived throughout the monitoring period. Gravel and Cooke (2008) present the first C&R biotelemetry study to combine biosampling and biotelemetry to integrate the multiple endpoints of physiology, behaviour and fate.

Migration and reproduction

The majority of biotelemetry research on C&R and migration has focused on adult salmonids. Anglers are easily able to target spawning migration routes because migration tends to be temporally cyclical and spatially predictable (McDowall 1999). Similarly for researchers, implementing a fixed station receiver array is often a practical solution for migrating species that follow characteristic routes and are returning to known spawning locations. Biotelemetry can be used to assess migratory behaviour, travel rate and mortality by using mobile tracking and/or fixed station receivers, or a combination of both methods. Tracking specific river reaches is particularly practical in systems where river length precludes simple mobile tracking (Whoriskey *et al.* 2000).

Catch-and-release biotelemetry allows for comparative studies to be conducted on migrants. For example, a C&R biotelemetry study was conducted to assess the consequences of C&R on the spawning migration fate of hatchery vs. wild steelhead trout (Oncorhynchus mykiss, Salmonidae) (Nelson et al. 2005). Comparative studies based on different treatment groups are lacking for migratory species. However, assessing the consequences of different handling and air exposure treatments on postrelease migration behaviour and fate is needed for migratory species. For migration studies. C&R biotelemetry can be used to assess short-term consequences of the angling event, for example by coupling analyses of behaviour and physiological stress (Thorstad et al. 2003) and long-term consequences, including assessments of changes in migration timing (Thorstad et al. 2007).

C&R biotelemetry and fitness

Studying fitness can be challenging in field settings, but is of crucial importance to judge the sustainability of C&R angling (Cooke et al. 2002a). Few studies have used C&R biotelemetry to examine fitness. Catch-and-keep fisheries preclude harvested individuals from passing their genes to subsequent generations, while C&R fisheries are intended to promote survival and hence fitness. However, C&R may still have indirect fitness-level consequences due to the inherent stress associated with an angling event, which may lead to indirect fitness costs such as reduced growth (Siepker et al. 2007), reproductive output (Ostrand et al. 2004) and in extreme cases, mortality. This is particularly salient for semelparous migrants, which only have one opportunity to spawn and in the event of en route mortality, would effectively have no spawning opportunities and no chance of passing their genes to subsequent generations, effectively resulting in zero fitness.

Using comparative biotelemetry to assess the effects of C&R on spawning behaviour and success is useful from an applied perspective to estimate the indirect fitness consequences of C&R on individuals,

and limited studies have been conducted to date. For species that engage in parental care behaviours, C&R may result in fitness consequences through sublethal alterations in behaviour and physiology during the spawning and nest-guarding periods, as these species are particularly vulnerable to capture during the reproductive period. For example, C&R biotelemetry revealed that nest-guarding largemouth bass that are angled from their nests will exhibit locomotory impairments for over 24 h following the angling event (Cooke et al. 2000). Lowerre-Barbieri et al. (2003) determined that common snook (Centropomus undecimalis, Centropomidae) that were caught and released exhibited changes in spawning behaviour, where angled individuals did not immediately leave a spawning aggregation but tended to move in and out of a spawning aggregation site more often. C&R biotelemetry allows for basic, and commonly indirect. measurement of fitness by assessing either postrelease mortality as well as allowing for an assessment of courtship, spawning migration behaviours and spawning success following angling. Ideally, however, fitness needs to be judged by directly observing reproductive output of caughtand-release vs. control fish in the field.

C&R biotelemetry and ecosystem-level consequences

Over-exploitation from anglers may lead to population or ecosystem-level consequences (Cooke and Cowx 2006; Lewin et al. 2006). For example, trophic cascades through the removal of key species can lead to community or ecosystem-level changes (Reynolds et al. 2002), even though C&R theoretically reduces mortality rates, compared to catchand-keep fisheries. Little is known about how systems-level changes occur as a result of C&R (Arlinghaus et al. 2007), largely due to the difficulty in measuring ecological outcomes. Biotelemetry alone does not allow for direct assessments of ecosystem-level consequences. However, this technology can be used in concert with other approaches to provide some understanding of the systems-level consequences of C&R. For example, telemetry can be used to assess interspecific behavioural interactions, such as foraging behaviour and predator-prey interactions (e.g. Cooke and Philipp 2004). By combining modelling techniques with telemetry data, it would be possible to estimate overall predation rates under various conditions.

This integrated approach could be used not only to determine when and under what circumstances a post-release predation event occurs, but also to assess the behavioural condition of the fish following capture. This is particularly useful for species that are prone to showing signs of impairment following release, such as bonefish (Cooke and Philipp 2004; Danylchuk *et al.* 2007b). Gaining an understanding of the ecosystem-level consequences of C&R is obviously very difficult to obtain in practice, but remains a high priority for managers (Lewin *et al.* 2007).

Experimental C&R studies using biotelemetry

Early C&R biotelemetry studies described the movement and behaviour of fish following release, but often failed to design comparative or experimental studies with multiple treatments and controls. More recently, comparative biotelemetry approaches have been used (e.g. Thompson 2007). Comparative studies that assess relative treatment effects provide useful information to managers and C&R tournament organizers and test the boundaries of stress resistance of fishes from a more basic scientific perspective. Comparative biotelemetry displacement studies generally compare return success and return rates by establishing a series of displacement groups at varying distances as well as one or more control groups (Richardson-Heft et al. 2000; Bunt et al. 2002). Comparative biotelemetry studies have been conducted on gear type to assess short-term survivability based on capture with I-style and circle hooks (Horodysky and Graves 2005). Nelson et al. (2005) used biotelemetry to compare the behaviour and survival of hatchery vs. wild steelhead salmon during their spawning migration. Danylchuk et al. (2007a) used biotelemetry to assess the short-term and long-term mortality associated with different handling and air exposure treatments on bonefish. In future, well-designed comparative biotelemetry studies must be conducted to ensure that results can be accurately interpreted and proper conclusions can be drawn for fisheries management.

Integrative C&R studies using biotelemetry

Integrative C&R studies that combine multiple endpoints, environmental conditions or intrinsic factors, such as nutritional state or genetics, are becoming more common in the fisheries research literature. Biotelemetry on its own allows for an assessment of behaviour and mortality, but when coupled with other endpoints, can provide considerable insight into the mechanisms of how C&R affects fish biology. These assessments have often been used in the laboratory, but there are few fieldbased studies. Although laboratory studies are also very useful in this context, they often do not permit the assessment of detailed post-release condition in natural systems, which is central to the study of C&R (Cooke and Schramm 2007). In a C&R context, findings from laboratory and field studies are not necessarily congruent with one another. For example, Cooke et al. (2003) found that largemouth bass exposed to simulated angling treatments and monitored using heart rate telemetry had different recovery profiles in the laboratory than they did in the natural environment. Extrinsic factors including environmental condition (e.g. water temperature, dissolved oxygen), predator-prey interactions, social behaviour and movement patterns may differentially affect fish responses to angling in the wild. These discrepancies warrant more emphasis on field-based approaches to understanding C&R consequences. Biotelemetry enables C&R researchers not only to extend laboratory-based findings to the field, but also to use telemetry tools to ask novel questions about the consequences of C&R.

A novel application of biotelemetry to C&R research is to link stress physiology with post-release behaviour and survivorship endpoints. Non-lethal biopsies allow for the assessment of prerelease physiological condition and biotelemetry allows for the assessment of post-release behaviour and fate (Cooke et al. 2005a; Skomal 2007). Nonlethal biosampling procedures commonly include the collection of blood samples to assess indicators of stress and exercise from plasma or whole-blood. Commonly measured endpoints include lactate, glucose, cortisol as well as changes in blood gases and pH and ionoregulatory status (Skomal 2007). Biopsies from other tissues can be collected nonlethally. For example, muscle tissue can be collected non-lethally and noninvasively to assess anaerobic energy stores (e.g. adenosine triphosphate, phosphocreatine and glycogen), but this technique has not yet been linked with biotelemetry in any published C&R studies to date.

Skomal and Chase (2002) and Skomal (2006) paired stress physiology with behaviour and survi-

vorship data from PSATs and acoustic transmitters to assess the consequences of C&R angling on large marine pelagic fish species. The authors tested hypotheses on post-release survivorship by examining the relationship between capture indices, such as duration of angling event, and changes in blood indicators of anaerobic metabolism and muscular fatigue, including blood pH, blood gases and lactate (reviewed in Skomal 2007). Biotelemetry results indicated that a recovery period of 2 h or less occurred immediately following release. Although mortality was low, Skomal and Chase (2002) and Skomal (2006) found that one bluefin tuna (Thunnus thynnus, Scrombridae) exhibited signs of severe lactacidemia and died immediately following release. However, this finding should be interpreted cautiously as two bluefin tuna that were exposed to longer angling bouts showed acid-base disruptions of a high magnitude vet survived throughout the monitoring period. Similarly, Lowe and Kelley (2004) studied the stress physiology and postrelease behaviour of caught-and-released California sheephead (Semicossyphus pulcher, Labridae). The authors found that plasma cortisol increased rapidly in proportion to the duration and intensity of handling and angling or trapping. Increases in plasma glucose, lactate (in angled fish) and insulinlike growth factor-binding protein were also observed. Acoustic telemetry data revealed that angled fish movement was limited for 12 h following release and no mortality occurred. However, within 18 h, fish began to recover, although recovery time depended on the intensity of the angling event (Lowe and Kelley 2004).

In the freshwater environment, two recent case studies have taken integrative and comparative approaches to the study of C&R by linking pre-release physiological condition with post-release behaviour and fate. Thompson (2007) combined externally attached radio transmitters and non-lethal blood sampling procedures to assess the response of largemouth bass to a range of air exposure durations and water temperatures. The author collected blood samples before and after treatment to assess changes in the concentrations of lactate, glucose, aspartate aminotransferase and Na⁺, K⁺ and Cl⁻ ions. Fish exposed to longer periods of air exposure had elevated plasma lactate concentrations and displayed postrelease behavioural impairments (e.g. tended to remain close to the site of release for longer durations and took longer to regain equilibrium) compared to fish exposed to shorter durations of air exposure.

Klefoth (2007) took an approach similar to that of Thompson (2007) by integrating short-term behavioural radio tracking with physiological condition for pike (Esox lucius, Esocidae) across different treatments. Treatments included exposure to various air exposure durations. Relative to controls, blood lactate levels were significantly higher in each of the treatment groups. Similar to that observed in Thompson (2007), behavioural impairments were observed in the higher duration air exposure treatments, where individuals showed significantly higher inactivity levels in the first hour after release compared to lower air exposure treatments and controls. The characteristic behavioural post-release recovery period observed in both of these studies following the C&R event is linked with the physiological recovery of fish resulting from long or intensive angling. The recovery period is likely a response to the severe anaerobic debt acquired during the angling fight (Wood et al. 1983) as blood lactate concentrations in most cases are correlated with angling duration and intensity. In the Klefoth (2007) study, biotelemetry revealed behavioural recovery within 24 h. similar to the results of Lowe and Kelley (2004) on California sheephead. In a C&R context, understanding the intersection of physiological and behavioural condition is necessary to reveal how fish respond to angling stress in the wild. The case studies described above illustrate how multiple endpoints can be easily and effectively integrated to provide a more holistic understanding of the consequences of C&R.

Challenges

The recent methodological and technological advancements of biotelemetry tools enable researchers to ask novel questions regarding the consequences of C&R. However, biotelemetry technology itself can have many challenges associated with its use. For example, with improvements in transmitter and receiver technology, transmitter failure rates tend to be quite low, but still occur. Selecting appropriate sizes and weights can be difficult, as transmitters that are either too large or have an uneven distribution of weight may affect swimming performance and behaviour (Bettoli and Osborne 1998; Cooke et al. 2002a; Zale et al. 2005; Weimer et al. 2006). Transmitters are commercially available in a variety of sizes and weights. The traditionally followed 2% rule (i.e. 2% body weight: transmitter weight) has recently been challenged and it has been suggested that the lowest possible weight be used, depending on the objectives of the study and the life stages and species used (Brown *et al.* 1999; Jepsen *et al.* 2005). With all telemetry studies, there are inherent biases towards selecting fish that appear in suitable condition to carry transmitters, which is not necessarily reflective of all fish that are released in C&R fisheries (Graves *et al.* 2002).

Cooke et al. (2002a) described a number of limitations associated with physiological telemetry, including challenges associated with transmitter implantation (e.g. electrode insertions in EMG surgeries). Another challenge includes the high cost of biotelemetry gear (transmitters, receivers and accessories). In many instances, particularly marine fisheries research, there are costs associated with hiring a ship and crew to deploy transmitters and/or track fish (reviewed in Skomal 2007). Cost can often be prohibitive or can limit total sample size of a study, particularly when using satellite technologies. Cost can be kept minimal when using transmitters with less sophisticated onboard sensors, although this is dependent on the research question that is being addressed in the study. In addition, there are inexpensive alternatives available, such as coupling basic positional transmitters with low-cost thermal loggers compared to costly onboard temperature sensors.

The effect of surgery or transmitter attachment on fish is one of the biggest limitations of telemetry studies (Pollock and Pine 2007). Transmitter attachment and presence can have a number of physiological and behavioural consequences (Bridger and Booth 2003) because telemetry requires the capture, handling, holding and attachment for external transmitters or insertion for gastric or surgically implanted transmitters. These processes are inherently stressful and can result in physical injury. Biotelemetry studies are based on the assumption that the implantation or attachment of transmitters does not affect fish after release. Identifying methodological vs. experimental consequences is a difficult task with biotelemetry (Jepsen et al. 2002; Bridger and Booth 2003; Cooke et al. 2004c; Wagner and Cooke 2005). Surgical insertion of transmitters requires fish to be anaesthetized and an incision to be made, which may lead to stress as well as secondary infections. Surgery effects can be minimized through practice by the surgeon. Transmitter attachment or implantation procedures should be optimized to reduce the duration of

surgeries and minimize holding and handling time. Where possible, efforts should be taken to minimize scale and mucous loss as well as to maintain sterile conditions to minimize the risk of secondary infections occurring (Bauer 2005; Bauer et al. 2005; Bauer and Loupal 2007). Surgeons should ensure that trailing antennas from radio transmitters do not abrade tissue. Air exposure durations should be kept to a minimum and fish should be constantly provided with fresh, flowing water over their gills that matches environmental water temperature and dissolved oxygen conditions. In addition, optimal dosages of anaesthetics should be used (Table 4) or where possible, anaesthetics may not be necessary, such as gastric tagging (Cooke et al. 2005a). Finally, fish should be rapidly released to locations where they are sheltered from predators.

Tracking fish can be a challenge in certain systems. Where possible, a large sample size may be useful to account for tag failures, fisheries harvest, predation and other circumstances. Consideration of a telemetry array can be very useful for tracking fish that move through predictable migration routes or closed freshwater systems. However, researchers must be aware of the technological limitations of their receivers and transmitters and must design their studies accordingly. Even with the advances in biotelemetry, there are still challenges with accurately assessing mortality (Pollock and Pine 2007) and determining the cause of mortality. For example, causes of mortality can include natural mortality, C&R consequences, surgery consequences, predation, fisheries harvest, emigration or transmitter failure (Hightower et al. 2001; Cooke and Philipp 2004; Waters et al. 2005). This can make interpretation of population-level consequences difficult for managers (Cooke and Schramm 2007). Researchers should define consistent criteria for mortality a priori for assessing mortality when tracking fish, such as defining zero movement within a certain number of days. Where possible, mortality can be confirmed using snorkelling/ SCUBA surveys in some systems. The development of improved mortality sensor technology should help mitigate this limitation. Goodyear (2002) reviewed a number of key limitations which affect C&R mortality estimates using pop-off technology.

Designing comparative studies can be challenging, as choosing appropriate control and treatment groups is often difficult. Researchers must select ecologically relevant treatment groups that highlight relative effects between treatments and use caution when designing control groups. Randomly allocating treatments is necessary in experimental studies. Similarly, developing integrative studies can also be difficult. While C&R biotelemetry permits the integration of multiple endpoints, studies that span multiple disciplines require communication amongst experts between disciplines to ensure appropriate methodologies are used. Research questions must be carefully developed in order to consider ecologically relevant endpoints and avoid autocorrelation between endpoints.

Finally, applied studies must be designed to effectively address management concerns. C&R biotelemetry studies often fuse basic and applied science by asking fundamental research questions while also, per definition, taking an applied approach (Young and Isley 2006). These studies require communication between researchers and managers from multiple jurisdictions (i.e. regions, countries) at all stages of the study (Arlinghaus *et al.* 2002, 2007). Maintaining communication with anglers, managers, policy makers and where appropriate, media sources, is necessary to promote the utility of C&R science and demonstrate the applied nature of this research.

Directions for future research

One of the major findings of this review is that the majority of C&R biotelemetry studies (Table 3) have focused on only a few game fish species. This trend is pervasive across recreational fisheries research in general (Cooke and Suski 2005). There are many opportunities to assess the consequences of C&R on lesser known species or species with lower economic value in many parts of the world (i.e. outside North America and Europe). Even within species, many inherent differences exist among individuals and populations which have rarely been considered in a C&R context, such as life history, age class, size structure and sex, which could benefit from biotelemetry studies. The challenge is that many commercially and ecologically important game fish species are often found in remote regions with poor access to the resources necessary to conduct biotelemetry studies. However, as telemetry technology continues to improve (e.g. improved battery life on receiver units), and new field-based tools become available, such as the field physiology tools used by Thompson (2007), researchers have a growing number of opportunities to study species or populations that were previously difficult to access.

This review highlights the paucity of C&R biotelemetry research that has assessed the ecosystemlevel consequences of C&R. However, conservation and management efforts are increasingly leaning towards 'ecosystem-based' approaches to managing fish populations. However, in closed systems, it is possible to use a telemetry array to create an 'ecological observatory' in the field (Cooke *et al.* 2005b; Hanson *et al.* 2007). This approach would enable researchers to assess individual behavioural impairments following C&R in relation to ecosystem-level interactions, such as foraging behaviours, and predator–prey interactions.

Although catch-and-keep fisheries result in harvested fish effectively losing the opportunity to pass their genes on to future generations, C&R fisheries may have fitness-level consequences that arise from stress which may lead to indirect fitness costs or indirect mortality. C&R fisheries are implemented, at least in part, as a means of promoting survival and fitness, angling-related stressors may lead to disturbances of homeostasis. Accordingly, there are opportunities for C&R biotelemetry research to investigate the sublethal consequences of C&R on fitness. Understanding the fitness-level consequences of C&R first requires an improved understanding of how fish are impaired following an angling event. This review points to the need for more integrative and comparative research to address these knowledge gaps. These types of studies will allow researchers to understand the factors that may preclude a fish from contributing their genes to subsequent generations.

A number of studies have assessed the consequences of C&R tournaments on fish. The majority of these studies have focused on displacement and little emphasis has been placed on understanding the multiple, interactive endpoints associated with C&R (but see Gravel and Cooke 2008), yet there are many opportunities to do so. For example, studies that assess pre- and post-release physiological condition (e.g. stress indicators) can be linked with post-release behavioural impairments and mortality at tournaments. There are logistical challenges associated with collecting data from C&R tournaments. Coordinating with tournament organizers can sometimes be difficult, especially in large tournaments. However, tournament organizers are generally keen on the science behind C&R and are willing to help researchers to carry out their studies. Similarly, tournament participants are often interested in assisting with collecting fish, which can result in large sample sizes of fish being caught in a relatively short time period.

There is considerable overlap between recreational C&R and commercial bycatch. In both cases, fish are captured, handled, exposed to air and often held onboard for prolonged durations prior to release (Cooke and Cowx 2006; Cooke and Wilde 2007). In both fisheries, fish can be brought from depth leading to barotrauma issues (Gravel and Cooke 2008). The physiological, behavioural and survival outcomes from both fisheries sectors share many commonalities (Cooke and Cowx 2006). Accordingly, there are novel opportunities for exchanging knowledge between these two sectors. For example, Moyes et al. (2006) coupled physiological indices with PSATs to assess the consequences of bycatch release on long-term condition and survival of large marine pelagics. Similar approaches have been used in a recreational fisheries context to link stress with behaviour and survivorship (Skomal 2006; reviewed in Skomal 2007). Recently, a study was conducted to assess the post-release behaviour of white marlin following capture on either commercial longline gear or recreational rod-and-reel (Horodysky et al. 2008). Similarly, Mäkinen et al. (2000) compared the consequences of capture by gill net and by rodand-reel. Future studies need to take a more multidisciplinary approach to the design of commercial and recreational fisheries studies and take advantage of the overlap between the two sectors. C&R and bycatch researchers should share collective knowledge and use previous research from both sectors to improve the design and implementation of future biotelemetry studies. In addition, inferences on the consequences of handling and capture stress can be made from general biotelemetry studies where fish have been captured using angling gear or comparable techniques. The general biotelemetry literature can be useful for identifying life stages or fish sizes that are more vulnerable to catch and handling stress.

Conclusions

Biotelemetry is a promising technology to aid in understanding the basic and applied aspects of C&R research. The number of C&R biotelemetry studies is growing rapidly and studies are becoming more diverse and integrative. There are many opportunities for future research, particularly with respect to developing comparative and integrative studies. Improvements in biotelemetry technology. including reduced size and weight and greater functionality (i.e. temperature/depth sensors), are permitting researchers to ask novel questions and gain greater insight into the consequences of C&R. Satellite technologies enable new data collection opportunities for comparative studies (e.g. for marine pelagic species). Integrating multiple endpoints permit the assessment of fish condition following an angling event. From both fundamental and applied perspectives, biotelemetry provides researchers and managers with an improved understanding of how fish respond to C&R. Although there are several challenges with applying biotelemetry to C&R research, C&R fisheries science has the potential to benefit greatly from this technology. C&R biotelemetry can provide more robust mortality estimates, permits the implementation of comparative studies, and perhaps most importantly, provides a platform for the integration of multiple C&R endpoints. Also, it offers a tool of relevance for linking disparate scientific disciplines such as stress physiology, behavioural ecology and applied fisheries science. Finally, stakeholders are appreciating that more research on C&R is conducted in the field under natural conditions, resulting in greater acceptance of field results among fisheries stakeholders. Biotelemetry offers a powerful means for the remote monitoring of free-swimming fish in their natural environments, but C&R biotelemetry is only in its infancy, and there remain innumerable opportunities for future research. Although biotelemetry alone cannot provide all of the answers for fisheries management, it can be used in conjunction with traditional fisheries management approaches to provide greater insight into the consequences of C&R.

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