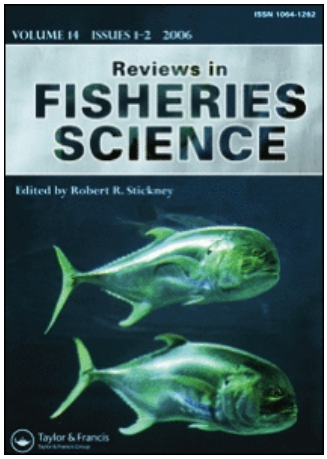

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Understanding the Complexity of Catch-and-Release in Recreational Fishing: An Integrative Synthesis of Global Knowledge from Historical, Ethical, Social, and Biological Perspectives

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Most research on catch-and-release (C&R) in recreational fishing has been conducted from a disciplinary angle focusing on the biological sciences and the study of hooking mortality after release. This hampers understanding of the complex and multifaceted nature of C&R. In the present synopsis, we develop an integrative perspective on C&R by drawing on historical, philosophical, socio-psychological, biological, and managerial insights and perspectives. Such a perspective is helpful for a variety of reasons, such as 1) improving the science supporting successful fisheries management and conservation, 2) facilitating dialogue between managers, anglers, and other stakeholders, 3) minimizing conflict potentials, and 4) paving the path toward sustainable recreational fisheries management. The present work highlights the array of cultural, institutional, psychological, and biological factors and dimensions involved in C&R. Progress toward successful treatment of C&R might be enhanced by acknowledging the complexity inherent in C&R recreational fishing.

Keywords angling, animal welfare, catch-and-release, environmental ethics, fishery management, hooking mortality, history, human dimensions, sublethal effects, recreational fishing, philosophy

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Introduction

Catch-and-release (C&R) angling[1] has a long history and has received increasing attention recently. It is not without its detractors, however, as we describe in detail in the present global synthesis. An integrative perspective that unifies historical, ethical, social, and biological aspects of C&R is considered essential to understand the complexity of C&R and offer a basis for its application in the management and conservation of recreationally exploited fish populations. In this article, we summarize and evaluate the available knowledge on C&R from a multidisciplinary angle, hoping to improve understanding of C&R, identify knowledge gaps, and make clearer the important research needs in C&R. The ultimate goal of the present work is to better inform recreational fisheries management decisions.

Context of Catch-and-Release

Fishing in general has increasingly been recognized as affecting global fish populations (NRC, 1999). Often, the public and academic discussion on the potential for fishing-induced declines of fish populations focuses on commercial fishing, particularly in the marine environment (Pauly et al., 2002). The notion that angling can impact fish stocks has been given less attention, but its role is increasingly recognized (McPhee et al., 2002; Post et al., 2002; Schroeder and Love, 2002; Cooke and Cowx, 2004; Coleman et al., 2004; Arlinghaus and Cooke, 2005; Cooke and Cowx, 2006; Lewin et al., 2006). However, the general awareness that recreational fishing can deplete fish populations is much older, as indicated by the implementation of minimum size limits and other rules limiting angler harvest since the Middle Ages in Europe (Policansky, 2002). In some ecosystems, particularly in many freshwater ecosystems of the temperate regions, but also in some coastal regions, recreational fishing has largely replaced commercial fisheries and thus is the sole user group of fish stocks (Arlinghaus et al., 2002). Consequently, for several species that are also of commercial importance, angling is today the largest source of fishing mortality (NRC, 1999; Coleman et al., 2004; Arlinghaus and Cooke, 2005; Lewin et al., 2006). Using estimates from Canadian recreational fisheries, Cooke and Cowx (2004) suggested that on a global scale, angling catch could be as high as 47.1 billion fish annually, of which about 17 billion are retained.

Angling and commercial fishing share many issues of relevance for management and conservation, such as fishing-induced trophic changes, reductions in biomass, age and size truncation, fishing-induced evolutionary changes, habitat impacts, pollution, and bycatch (Cooke and Cowx, 2006). There are also some striking differences. For example, compared to a large trawler in the ocean, a single angler is characterized by a low catch rate. By considering millions of anglers world-wide, however, their cumulative impact can be high (Cooke and Cowx, 2004, 2006; Lewin et al., 2006). Another difference between an angler and a commercial fisher is the economic incentive to fish. A commercial fisher will sooner or later stop fishing or reduce fishing intensity if the catch does not offset the cost. The "survival" of an angler, however, does not necessarily depend on high catch rates, although the ultimate product of the angling experience, angler satisfaction, is often catch-dependent (Arlinghaus

[1]We use the term *angling* synonymously with recreational fishing, i.e., fishing that does not generate resources to meet physiological needs essential for human survival (e.g., nutrition) and for which obtaining food or selling fishing products to offset cost is not the primary motivation. In western cultures, recreational fishing is typically conducted with hook, line, and rod, often including a reel, during free time (as opposed to working time), does not involve selling fishing products to generate income, and is subjectively defined by the individual participant as being leisure; it is therefore non-commercial. We refer to participants in recreational angling as *anglers*.

and Mehner, 2005; Arlinghaus, 2006). Therefore, anglers might continue fishing even if the catch opportunities are low due to overfishing or other impacts such as habitat alterations leading to stock declines.

Post et al. (2002) proposed that some recreational fisheries are not self-regulating, i.e., anglers do not necessarily reduce fishing when stocks decline. So-called depensatory processes increase the probability of fish-stock collapses in populations exploited by anglers (Post et al., 2002). Depensatory processes involve an increasing per-capita mortality probability at low population abundances. In recreational fishing, depensation can occur due to inverse density-dependent illegal harvest rates (Sullivan, 2002) or inverse density-dependent catchability (Post et al., 2002).

One frequently applied and promoted means to cope with high angling effort is C&R angling (Barnhart and Roelofs, 1977, 1987; Policansky, 2002). In a sense, C&R angling is equivalent to bycatch and discarding in commercial fisheries (Cooke and Wilde, in press), although the definition of bycatch does not apply if an angler releases a fish that was intentionally caught, which is often the case. Due to the nature of the capture method, fish typically experience less damage when captured by angling than when caught by most commercial fishing gears such as seines and gill-nets. Therefore, releasing fish in comparatively good condition is more likely in recreational fishing than in most commercial fisheries. Consequently, the option for C&R fishing, if properly applied, provides a fishery management answer to potential angling-induced impacts on fish population (Lucy and Studholme, 2002).

From a fisheries management and conservation point of view, common sense would suggest that implementing C&R encourages the biological, economic, and social sustainability of recreational fishing, and much evidence shows that it does (Policansky, 2002). For example, by releasing fish, the impact of angling on the resource is minimized while, at the same time, providing important social and economic benefits to society (Arlinghaus et al., 2002). This perspective, however, overlooks ethical issues with C&R, cultural and legal conflicts associated with some forms of C&R (Arlinghaus, 2005; in press), and manifold biological impacts that might take place if C&R is conducted inappropriately (Cooke et al., 2002a; Cooke and Suski, 2005).

Definitions

C&R refers to the process of capturing fish by using hook and line, mostly assisted by rods and reels, and then releasing live fish back to the waters where they were captured, presumably to survive unharmed. C&R is a relative term and implies a gradient from C&R only to catch-and-kill (harvest) angling (Policansky, 2002). It can be a voluntarily action or the result of harvest regulations, i.e., mandatory (Quinn, 1996). Over time, the use of the term has broadened from a "no kill/zero limit" principle to include the use of special regulations, including size (minimum, maximum, slot) and bag limits that force anglers to release part or most of the fish caught.

In its most extreme form, total C&R, every fish caught by an angler is released alive; to the degree possible, the fish are released unharmed. Regulatory C&R refers to C&R that is required by regulations such as length-based limits (i.e., all fish smaller or larger than the specified size limit must not be retained, and therefore must be released), protected seasons, bag limits, protected species (e.g., some species are protected and cannot legally be retained), etc. Voluntary C&R refers to the voluntary decision of an angler to release fish. It can be total or not, but it is not mandated. For example, an angler might retain only one fish of a desired species and size and voluntarily release all others.

In this article, we use the term C&R to refer to any form of C&R discussed above. It does not mean only total or voluntary C&R, unless specifically stated.

Magnitude of Catch-and-Release

Globally, millions to billions of fish are released after capture by recreational anglers each year. Rough global release rate estimates are about 60% (Cooke and Cowx, 2004). In the United States alone, in 2000 an estimated 11 million anglers participated in 78 million marine fishing trips and caught 445 million fish, of which 253 million or 57% were released (Bartholomew and Bohnsack, 2005). The proportion of caught and released fish has increased from 34% of the total catch in 1981 to 59% in 1999 (Bartholomew and Bohnsack, 2005). However, there is much diversity in C&R rates in different cultures, institutional environments, situations, and species, with little room for reliable estimates that apply in general. Angling for non-salmonid species in the U.K., so-called coarse fishing, is an example of an extreme form of C&R, in which almost all fish are released (North, 2002). The same is true for some species-specialized fisheries around the world, such as big game angling in the United States, e.g., Atlantic white marlin, *Tetrapturus albidus* (Cramer, 2004); bonefish, *Albula* spp. (Policansky, 2002); steelhead, *Oncorhynchus mykiss*, in North America (Policansky, 2002); and carp, *Cyprinus carpio*, in much of Europe (Arlinghaus and Mehner, 2003). Release rates can also be as low as near 0% if caught fish are used for human consumption. This is, for example, the case in many recreational fisheries in Eastern Europe and in many parts of Northern Europe. Because most recreational fisheries in industrialized countries are today managed based on some variants of length-based size limits (Arlinghaus et al., 2002), C&R, in one form or another, is a day-to-day practice in contemporary recreational fisheries and is mandatory for specific species or sizes.

Rationale

Because of its appeal of conserving exploited fish populations while maintaining angling use, C&R has been adopted to varying degrees by anglers as well as by fisheries managers to reduce the (presumed negative) effects of angling on fish populations (Policansky, 2002). C&R has several meanings for anglers, conservationists, managers, scientists, and politicians. It can mean a harvest regulation, a management strategy, an angling philosophy, and, for some specialists anglers, a strict religion (Aas et al., 2002). From the angler's perspective, it can be conducted for conservation purposes to preserve fish for their own sake (non-consumptive motive) or for conservation purposes to preserve the opportunity for recapture (consumptive motive, Arlinghaus, 2005).

From the biological perspective, understanding the lethal and sublethal impacts of C&R either on the individual or the exploited population is the focus of applied research. From a human dimensions perspective, two additional aspects of C&R are particularly important to understand: 1) the ethic of voluntary C&R cross-culturally and within a particular angler community, and 2) the illegal harvest of protected fish under regulatory C&R. Illegal harvest by anglers can lead to a decline of the fishery if, for example, immature fish are killed in significant amounts (Sullivan, 2002). In contrast, under voluntary C&R, an angler voluntarily decides to not harvest a fish and thus, consciously or unconsciously, contributes to resource conservation. The conditions that favor or disfavor this propensity are manifold, species- and situation-specific, with limited room for predictions about the C&R behavior of anglers that apply generally (Ditton, 2002).

However, understanding the institutional and social dynamics leading to voluntary C&R behavior or acceptance of regulatory C&R is crucial for improving the implementation of C&R management policies. For example, in Germany the Animal Protection Act has resulted in a social norm to kill each fish that is not protected by size limits or protected seasons (Arlinghaus, 2007). In such an environment, implementation of scientific insight showing how to ameliorate the impact of C&R becomes difficult or even impossible. The same is true for fishing cultures that resent releasing fish on cultural grounds (Jones and Williams-Davidson, 2000; Lyman, 2002; Policansky, 2002; Aas et al., 2002; Wolfe 2006). In such cultures, promoting C&R practices can result in conflict within the angling community and between different sectors with interests in the well-being of fish (Lyman, 2002; Arlinghaus, 2007; Wolfe, 2006).

Previous research on C&R has rarely been integrative in orientation and thus has not coupled the social with the biological sciences cross-culturally to provide a complete and global perspective. Much of the previous work has focused on one specific aspect of C&R-hooking mortality (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005). No form of angling entails zero risk of mortality for the fish, so C&R with 100% survival rate of the released fish is an ideal rather than a practical reality. Consequently, survival rates or alternative mortality rates of released fish have been and are a major focus of C&R science. Most of the available peer-reviewed papers estimate hooking mortality of released "sport" or "game" fish, which means that research is available mainly for a limited number of highly valued recreational species (Cooke and Suski, 2005).

Depending on the gear used, the species of fish, the angler's skill and intentions, and many environmental factors, hooking mortality can range from less than 1% to >90%, the latter, for example, if fish are hooked in vital organs (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005). Although hooking mortality has been studied under many conditions for many fish species, much is still unknown, and relatively little is known about sublethal effects such as loss of status of a hooked fish in a social hierarchy, physiological changes, decreased reproductive success, altered behavior, and decreased growth rate (Cooke et al., 2002a). Hooking mortality was first reviewed by Muoneke and Childress (1994), but no paper has reviewed hooking mortality along with additional aspects associated with C&R such as historical development, ethical perspectives, the social dimension, economic factors, and sublethal impacts on the released fish. Some more recent syntheses have been published on specific aspects of hooking mortality (e.g., Cooke and Suski, 2005; Bartholomew and Bohnsack, 2005) and on the history of C&R in North America (Policansky, 2002), but no comprehensive review on hooking mortality and the factors influencing it is available that covers the globe. Less biological research is available on potential sublethal impacts of C&R, and most C&R research has focused on selected species such as largemouth bass (*Micropterus salmoides*), striped bass (*Morone saxatilis*), Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*), and walleye (*Sander vitreum*, Cooke and Suski, 2005).

Another line of research has tried to understand the human dimensions of C&R, most often from a socio-psychological research perspective in the United States (Sutton, 2001). Understanding C&R in any one country is complex because many people fish for various reasons (Fedler and Ditton, 1994; Arlinghaus and Mehner, 2004) and have various cultural backgrounds (Lyman, 2002; Wolfe, 2006). The boundaries between angling, commercial fishing, and subsistence fishing can be blurry at times (e.g., NRC, 2005). Studying C&R across countries is more complex because the history, laws, culture, economic environment, and many other factors differ from one country to another, even as the reasons and ways that people fish vary within countries. For example, for some stakeholders, releasing fish is

a reprehensible practice because C&R is viewed as "playing with fish for no good reason" (Aas et al., 2002; Lyman, 2002; Policansky, 2002; Wolfe, 2006). By focusing research only on the biological aspects or exclusively on the social psychology of the voluntary C&R behavior of anglers, the complexity of the issue is lost, and limited insights can be gathered to understand the diverse nature of C&R fishing from an integrative perspective. Such an integrative perspective is needed for improving the science supporting successful fisheries management and conservation; facilitating dialogue among managers, anglers, and other stakeholders; minimizing conflict potentials (Arlinghaus, 2005); and paving the path toward sustainable recreational fisheries management; among other reasons.

Objective

The objective of this article is to provide a cohesive, synthetic view of C&R, including historical, ethical, social, and biological perspectives from around the globe. The basis of our syntheses is on peer-reviewed literature, acknowledging that important gray literature on C&R is available, much of which is not covered here. We do not focus on particular species, ecosystems, or environments (e.g., inland waters), types of fisheries, or nations. Instead, we document the current state of knowledge of C&R from the broad cultural perspectives of an international group of authors, even as we recognize that many cultures are not included in our group. However, the group hails from Europe, North America, and Australia, and has research experience from other parts of the world. We also comprise a variety of scientific disciplines, which we take advantage of in this article to summarize historical, ethical, social, biological, and other knowledge to document the diversity of perspectives and identify further research needs. Our aim is to help inform fishery management of policy and societal decisions.

We begin with a historical overview of C&R. A section on ethical issues involved in C&R around the world follows, because ethics and institutions (i.e., formal and informal rules-in-use), which are expressions of the culture of particular societies, set the ultimate constraint on the implementation of any C&R policy and because questions about right and wrong (ethics) shape how society and members of society (anglers) view and approach C&R. The paper then documents the social and biological dimensions of C&R. Questions to be answered include what angler types and underlying personal traits promote adherence to C&R, what factors facilitate the severity of lethal and sublethal impacts of C&R, and how those factors can be ameliorated. A separate management section elucidates documented potentials and pitfalls of C&R policies. This section is intended to discuss issues rather than provide a thorough review of papers that have evaluated regulatory changes involving C&R (e.g., changes in minimum size limits). Such a review is beyond the scope of our analysis. Finally, some future areas of research are outlined.

Origin of Recreational Fishing and Catch-and-Release

Understanding the origin of C&R fishing requires a historical context because voluntary and regulatory C&R is restricted to recreational fishing but not always associated with it (e.g., total catch-and-remove angling irrespective of fish size). We therefore begin with a discussion on the origins of recreational fishing that involve some form of C&R.

Fishing techniques that involved hooking the fish (angling) were invented at least 50,000 YBP (years before present), primarily to catch fish for food (Sahrange and Lundbeck, 1992). The first evidence of angling as a recreational activity not motivated by personal

consumption, sale, or trade derives from an image from 3,290 YBP displaying an Egyptian noble (Pitcher and Hollingworth, 2002b). The ancient Greeks and Romans regarded recreational fishing as fit only for slaves and children and a temptation to be avoided (Pitcher and Hollingworth, 2002b). They also considered fish species found in springs or clean flowing waters to be sacred to the gods or goddesses because clean water was rare around the Mediterranean. Accordingly, angling was not done for many freshwater species (Radcliffe, 1926, p. 201). Nevertheless, recreational fishing was common during that time, particularly among wealthy people (Haase, 2000). It is not clear to what degree C&R was involved.

Although there are earlier references to releasing a portion of one's catch, we confine our discussion to the origins of recreational fishing and C&R to the Middle Ages in Europe and England, as there is little documentation from earlier times and England seems to be the origin of voluntary C&R. Roman Catholic Europe, the emerging class structure in England, and the early history of the United States produced similar but distinct hook-and-line recreational fishing cultures despite some interactions, and they generated different responses to fish and the practice of C&R.

Europe

Under *Res Communes* from Roman law, flowing waters and their fishes were public property. Because medieval Europeans consumed great quantities of fish, fishing pressure increased in relation to population growth (Hoffmann, 1996). By the 13th century, legislators were already complaining about overfishing. As a result, privatization of previously common or public fishing rights was widespread in much of medieval central Europe (Hoffmann, 1995). By about the year 1200, grants from kings or simple seizure put landowners in possession of all but the largest inland river fisheries (Hoffmann, 1996). Between 1200 and 1400, markets and fishing rights developed. One-time lordly servants evolved into full-time fishers who paid annual monetary dues or, rarely, a share of the catch for the right to exploit the lord's water (Hoffmann, 1995). In this context, fishing with rod and line was one means to appropriate fish for personal consumption and despite its subsistence component was similar to modern recreational fishing. The *Heidelberg Fishing Tract* (1493) is among the earliest extant works on recreational fishing. One of its regionally published forms, the *Tengresse Fishing Tract*, contains not only complete instructions on how to catch fish and where to find them but also the recipes for fly patterns (Hoffmann, 1997); the first artificial baits were, however, invented by Romans (Hensel and Vogel, 1978). In the Middle Ages, development of recreational fishing and its popularity were linked to the art of printing (1440 A.D.) and the associated publication of angling books (Hoffmann, 1997). The first clear reference to angling as distinctly recreational occurs in the *The Country Farm* (1307, Italy; Estienne, 1616). It refers to angling equipment "and . . . the seasons and time of the year fittest for the sport." The term "sport" fishing often used synonymously today with recreational fishing derives from the verb "to disport," which means to take one's ease, to re-create. It was used in England to refer to all forms of recreational activities and field "sports," including recreational angling. In the 18th century, "to disport" was replaced by "to sport" in England and thereafter also taken over into recreational fishing terminology in mainland Europe (Körbs, 1964). It is different from the modern definition of sport because only particular forms of recreational fishing, such as competitive fishing, can be described as sport in the modern context of competitive sport science (Heister, 2005).

Fishing for food and recreation greatly increased in popularity in the 19th and 20th centuries. In Germany, recreational fishing was popular but did not have the same social

status as other chivalrous activities such as shooting, climbing and hunting (Krüger, 2004), a situation that is similar today. It is not entirely clear how much C&R fishing, either regulated or voluntary, took place in the Middle Ages, but minimum-size regulations and seasonal closures in England (Policansky, 2002) and in France (Mascall, 1590, cited in Marston, 1903), required the release of some fish.

Catch-and-Release in England. Fishing for food has a well-documented history in England as well, and regardless of developments noted below, fish have always been relied on as food by most Britons, leading to a prohibition of weirs on all English rivers even in the Magna Carta (1215 A.D.) (Getzler, 2004, p. 21).

The first reference to releasing fish in English literature appears in the ploughman stories, beginning in the 15th century (Piers of Fulman, 1420, cited in Merwin, 1995). In *A Treatyse on Fysshynge wyth an Angle* (originally written around 1420, but not published until 1496), Dame Juliana Bernes[2] argued for conservative harvest to protect the resource (McDonald, 1963). But recreational fishing in those days was a gentleman's sport, not typical of the common people.

The plague of 1348 killed a third of the population in England. It followed hard on the first decades of the little ice age, the decline of feudalism, and the advent of the cash economy. Many of the serfs who had been forced off the land and into cities chose to return to lives of farming and subsistent hunting and fishing in the largely empty countryside. Qualification statutes were quickly imposed that prevented people who needed fish and game as food from taking them. Hunting was reserved for the ruling class, specifically to prevent peasants from returning to a subsistent lifestyle in a rural England with no fences, few defined land holdings, and a greatly diminished population. In the new England of the late Middle Ages, commoners' labor was needed for mills and farms. The Statute of Laborers (1351) required commoners to work. They were not allowed to fish or hunt for their food: "None shall hunt but which have sufficient living" (Lund, 1980, p. 8, 22). One of the demands of the Peasants Revolt of 1381 was the return of the right to fish in the River Ver (Herd, 2003).

About one hundred years later, Wynkyn de Worde, the publisher of the *Treatyse*, wrote that the little work on fishing was published with the text on heraldry and falconry to keep it out of the hands of "every idle person who would desire it" (McDonald, 1963). When viewed against the historical background of depopulation and hardships and the subsequent imposition of the qualification statutes for the taking of fish and game, these early references to releasing fish and conservative harvest may well represent the origin of the idea that releasing a portion of one's catch was the mark of a gentleman.

During the period between *A Treatyse on Fysshynge wyth an Angle* (1496) and Izaak Walton's first edition of *The Compleat Angler* (1653), little was written about fishing except for simple retellings of Bernes's material (Marston, 1903; Gingrich, 1974). Early editions of Walton (1653 onward) contain no reference to releasing fish. Although he lived a life of some ease, Walton was a commoner and a lifelong member of the ironmonger's guild. In *The Compleat Angler*, he kills his catch, but he does speak for conservation.

For the fifth edition of *The Compleat Angler*, Walton asked Charles Cotton, a younger gentleman, to write a section on fly fishing; this contains a specific reference to voluntary C&R: "This is a diminutive gentleman, e`en throw him in again, and let him grow till he be more worthy your anger." This line is noted in a later popular edition of *The Compleat*

[2]Dame Juliana's name is spelled in various ways, usually Bernes, Barnes, or Berners. There is almost no evidence of her existence as an angling writer, and her name almost certainly is a pseudonym (Blades, 1881; McDonald, 1963; Schullery, 1987, 1999).

Angler (Walton, 1853, p. 288) to establish Cotton as a "real sportsman" for "He contemns catching small fish" and says "throw them in again."

Cotton's contribution to *The Compleat Angler* was written soon after the English Civil Wars. Those dissenters who survived King Charles II's purges were prohibited from hunting by the Game Act of 1671, which allowed only Protestant gentry earning over 100 pounds annually from their lands to hunt. The act effectively kept the opposition, Catholics, and the less well-to-do from practicing with the new technology: firearms. The remaining gentry and the rapidly growing merchant class had only fishing to elevate themselves as gentleman-sportsmen. What better way for the rising merchant or disenfranchised gentry to show that they were truly of the upper class than to not need one's catch as food? Release some fish, thereby giving credence to the 1853 edition's interpretation of Cotton's instructions as those of a gentleman. Even so, most anglers killed most of the fish they caught, and regulations mandating releases increased. In the reign of George II (1727–1760), size limits for roach (*Rutilus rutilus*) were also imposed, and it was illegal to take, possess, or sell any undersized fish or fish caught out of season (Policansky, 2002).

In *The Compleat Angler,* Izaak Walton quoted a popular phrase: "Everyman's business is no man's business" (Walton, 1853), which is a clear account for the concerns much later described as "the tragedy of the commons" (Hardin, 1968). The English solution to this problem of overexploitation was to pass the Acts of Enclosure. Starting in the early 1700s, the acts were initially imposed to allow larger landowners to consolidate their holdings within boroughs, thereby increasing their yield though efficiency of effort. As all landowners had to pay for the needed surveys, thousands of small-tract farmers who could not afford the surveys were forced from the land to urban centers, an intended result of the Acts because workers were needed for the growing number of mills. The Industrial Revolution led to further increases in the number of mills on many rivers, along with the need for manpower (Getzler, 2004). The Acts of Enclosure's final iteration, passed in the 1840s, specifically prohibited all but owners or their assignees from fishing most waters. These acts were so onerous and had such impact that they were published in a children's fishing tract, with punishments for poaching, including fines, jail time, or deportation (Salter, 1841). The Acts of Enclosure contained the most significant reduction of the public's right to fish, and its effect was greatest just as the "Nation of Shopkeepers" was gaining the leisure needed to pursue field sports in the 18th and 19th centuries (Herd, 2003). Similar developments occurred in central Europe: fishing became a private right coupled with rigorous regulations leading to regulatory C&R.

As fly fishing became more regimented in 19th century England as the exclusive activity of the well-to-do or well connected, writers increasingly mentioned releasing a portion of one's catch voluntarily. Sir Humphrey Davy wrote of the questionable morality of all field sports and then defended recreational ("sport") fishing with: "Every good angler, as soon as his fish is landed, either destroys his life immediately, if he is wanted for food, or returns him to the water" (Davy, 1970, reprint from 1828, p. 11). The most popular angling author of the mid-19th century wrote of the need to let out-of-condition fish go to grow fat and healthy (Francis, 1995). By 1913, Halford could declare that "the sportsman is not only willing to return any below the legal limit of the water, but exercises great care both in extracting the hook and returning the fish to the water" (Halford, 2000, p. 309). And it was an Englishman of little regard in the fishing world, Lord Baden–Powell, who did most to popularize C&R in England. The hero of Mafeking and the founder of the Boy Scout movement later became an ardent angler (Baden-Powell, 1986). Revered by millions of boys worldwide between 1900 and 1939, Baden-Powell preached the gospel of C&R wherever he fished (Precourt, 1999). He wrote of the need to let fish go so that other anglers might have good sport, that

fish might grow and reproduce, and that the reason for recreational fishing is to renew and recreate more than it is to catch fish.

The English were therefore probably the first to practice voluntary C&R as an ethic and during fishing competitions, two aspects that need to be distinguished today. The English also developed the so-called coarse-fishing ethic, voluntarily releasing almost every non-salmonid fish (North, 2002). Late in the 20th century, the British coarse-fishing ethic found considerable support in Europe, with many highly committed anglers and angler groups practicing voluntary C&R (Policansky, 2002; Arlinghaus and Mehner, 2003).

Regulatory C&R appears to be much older and related to the implementation of the first regulations throughout Europe. But C&R in Europe has a variety of origins and traditions (Aas et al., 2002), which complicates its analysis. Perhaps of greatest relevance here is that in mainland Europe, the view that C&R is "an unethical and reprehensible fishing practice" is much more common than it has been in England and North America, although there are some who view it as "both an ethical and conservative approach to resource utilization" (Aas et al., 2002).

Finally, there are private regulations to maintain recreational fisheries in angling clubs and associations that are derived from a 19th-century English perspective. Club or beat rules limit the angler's number of days on water. Other rules may require only fishing upstream with the dry fly to rising fish and may require sharing a rod with a companion. These private rules have long been the way that angling associations established C&R on private waters in England (Robson, 1998) and have aspects of both voluntary (because they are not imposed by government) and regulatory (because they are imposed, albeit by general consent) C&R.

North America

During the waves of immigration from Europe that descended upon North America in the 1800s, the European tradition of access to fish resources as food combined with the distinctly American public ownership of fish and game led to excessive harvest on public and private lands. Harvests by immigrants simply compounded already excessive takes of fish by established anglers and commercial interests. As early as 1734 there was a law limiting fishing to "angle-rod, hook and line" in New York. In 1822, Massachusetts law prohibited fishing for brook trout, *Salvelinus fontinalis*, except with hook and line (Reiger, 2001, p. 17). And the growing percentage of Roman Catholics in the United States climbing from 5% in 1850 to 17% by 1906 (Byrne, 2006) consumed fish nearly half the year in accordance with their religious heritage. Conservation grew from many reasons such as the tradition of the gentleman sportsman in response to loss of fish and wildlife (Reiger, 2001) and from pockets of immigrants with common cultural roots who grew concerned over attempts by urban interests to consolidate rural holdings and strip them of their resources (Judd, 1997). Irrespective, the American Civil War, at more than one million casualties, the costliest in U.S. history? squelched nearly all early efforts to conserve fish and wildlife.

In the years after the Civil War, the United States turned to nature to heal, as other cultures have done from at least the 15th century (Walton, 1835; Blades, 1881; McDonald, 1963). The first American publication on fishing (Seccombe, 1739) established fishing as the best way to re-create oneself for the Lord's work. The universal theme of healing and renewal through nature appealed to thousands of Americans sick with the pain of the Civil War.

Two years after the Civil War, a preacher from Boston known as "Adirondack" Murray, published *Adventures in the Wilderness* (Murray, 1869). It extolled the healing virtues of nature to a recovering nation while increasing numbers of Americans lived in burdensome

urban situations. The book was immensely popular, going through eight printings in its first year. "Murray's fools" rushed from cities in droves each summer, seeking the healing balm of nature (Schullery, 1987). During this period of declining fish stocks due to industrialization, pollution, commercial fishing, and recreational fishing excess, many writers emphasized the need for conservation (Halprin, 1987). The powerful image of nature-as-healer was reflected in the lives of three of America's most influential 19th-century conservationists: John Muir, Theodore ("Teddy") Roosevelt, and Gifford Pinchot (Schullery, 1993; Miller, 2001)

Nature-as-healer has resonated with many Americans from the Civil War onward. In addition to this is the even older American idea that nature is to be subdued. From our earliest times, the American frontier hero bends nature to his will, an idea that persists even today, more than a century after the frontier's closing (Limerick, 1988).

Catch-and-Release in North America. The two seemingly opposite myths combine in voluntary C&R to allow American anglers to both best nature (catch the fish) and be "healed" through nature (release the fish), with C&R being a visible demonstration of respect for nature (Evans, 2005). This subject is too fragile for this survey, but those interested in healing through nature should pursue issues surrounding mythic archetypes involved in outdoor sports.

Many Americans have appreciated the value of releasing a portion of their catch emotionally from the very first truly American fishing book (Norris, 1864). In the first decades of the 20th century, many angling books included references to the need to release fish (Schullery, 1987). Two angler-authors, Pearl Zane Gray (1975–1939) and Roderick L. Haig-Brown (1908–1976) greatly influenced the development of the angling conservation ethic and the "raison d'etre" for voluntary C&R (Radonski, 2002).

By 1939, as part of a conversation among sportsmen stretching back nearly a hundred years, Lee Wulff would write: "There is a growing tendency among anglers to release their fish. Game fish are too valuable to be caught only once" (Wulff, 1939, p. xv). Indeed, today in the United States, voluntary C&R is the norm among many American freshwater anglers and increasingly common in saltwater as well (Policansky, 2002; Lucy and Studholme, 2002; Salz and Loomis, 2005). However, everything changes. In recent decades, immigration to the United States from Europe has been overtaken by immigration from the rest of the world. These new Americans represent many cultures with deeply held traditions of fish as food and different, though equally strong, cultural values surrounding fish. Concern about the ethics of C&R has been rising in North America for several decades (Policansky, 2002).

Conclusion

The need to release a portion of one's catch was written about in America as early as 1864. Concerns for conservation in America during the 19th century led to acceptance of C&R as a means of preserving stocks of fish. This was part of a dialogue stretching back hundreds of years. Great forces, the Civil War, and immigration from Europe helped to change public attitudes toward nature in America. This contrasts sharply with the continental European tradition of fish as food.

English-speaking anglers (North America, Great Britain, Australia, and South Africa) are today the cultures in which C&R, particularly voluntary C&R, is accepted to a great extent, but it is accepted to some degree in other cultures as well. However, there is great diversity in public attitudes toward C&R, particularly total C&R (Aas et al., 2002; Policansky, 2002; Arlinghaus, 2007). Even today, American anglers are reluctant to mention releasing fish in some places. In Alaskan villages, educators rarely speak of C&R, referring to

selective harvest instead (Lyman, 2002). Andy Royer, the supplier of much of the Tonkin bamboo used in fine rod building in America, is still reluctant to tell his suppliers in China about American anglers who release the fish they catch (Duncan, 2005). In Scandinavia, the angler who returns to camp with no fish for the cook is regarded coolly by fellow camp members who were expecting the angling to result in food (Aas and Kaltenborn, 1995). Many anglers from Eastern Europe think similarly, as evidenced by conflicts between Germans who favor selective harvest and immigrants of German descent from countries of the former Soviet Union who are accustomed to fishing mainly for food; these conflicts concern catch-and-kill versus C&R of selected species (Arlinghaus, personal observations).

In Europe, although C&R is today firmly integrated in the angler's lifestyle in some countries (e.g., U.K., The Netherlands), in other countries, such as Germany, releasing legally sized fish voluntarily C&R risks public prosecution in conflict with the Animal Protection Act (Arlinghaus, 2007). In contrast, regulatory C&R, particularly of undersized or otherwise protected fish, is today almost universally accepted as a "good idea" to conserve fish stocks and fishing opportunities.

Voluntary C&R in Europe and elsewhere seems to be growing with the spread of the British so-called coarse (i.e., non-salmonid) fishing ethic and the so-called "specimen-hunting" practiced by many of the highly committed and often species-specialized angler groups (especially carp; northern pike, *Esox lucius*; salmonids; or European catfish, *Silurus glanis*), which are supported by species-specific specialized magazines and angler organizations (e.g., German Pike Angler Group). They strongly adhere to voluntary, often total C&R, as do some of the competition or "match" fishers across Europe (North, 2002). This is accepted in some cultural environments, but less popular in others. Strong subsistence thinking prevails particularly in eastern Europe, northern Scandinavia (Aas and Kaltenborn, 1995), northern North America (e.g., NRC, 2005), and in most marine recreational fishing outside the English-speaking world. Understanding and promoting C&R is therefore intimately linked with associated culture and institutional constraints. This ultimately opens the discussion about the ethics of voluntary C&R, which is hotly debated around the world (De Leeuw, 1996; List, 1997; Balon, 2000; Aas et al., 2002, Policansky 2002).

Ethical Aspects of Catch-and-Release

Armed with net and bucket, children all over the world go for a paddle on the beach. They catch little fish and other animals, look at them, swap them, proudly present them to their parents, and eventually release their catch into the sea. In the process, some of the critters get hurt, some die, but most of them probably survive. The seemingly harmless pleasure at the beach is a case of C&R. Paddling may not qualify as recreational fishing, but the ethical issues encountered are in both cases very much the same. The core question is concerned with the morality of recreational fishing that involves some form of catching and releasing a fish and the problems this might entail, e.g., for the well-being of the released fish (De Leeuw, 1996).

C&R angling is one of the many aspects of recreational fishing. In the wake of the animal rights movement and society's concern for the well-being and welfare of animals, C&R angling has come under considerable pressure on ethical grounds (Spitler, 1998; Balon, 2000; Huntingford et al., 2006). For example, in a review on the assessment of the welfare issues associated with aquatic animals, Håstein et al. (2005) state that on moral grounds, fishing for subsistence might be acceptable, while angling, including C&R, may not. Representative of the general thrust of the accusations on the academic level is De Leeuw, who claims that anglers need to find a justification for their cruel treatment of fish

(De Leeuw, 1996). On the popular level, the animal rights organization PETA (People for The Ethical Treatment of Animals) tries to win people over with slogans like "Fish have feelings, too." Cruelty captures academic and popular imagination, but cruelty is merely one facet in a wider picture. In order to fully appreciate the content and the different positions in the debate about recreational fishing in general, and C&R in particular, that wider picture needs to be sketched.

Underlying the discussion about angling are issues in the field of environmental ethics (Evans, 2005). Environmental ethics deal with the moral relationship of humans to nature. Ever since the ancient Greeks, there have always been philosophers thinking about humans and their environment (Coates, 1998), but the sheer volume of output since the 1960s surpasses, at least in quantity, everything that has gone before. This surge was triggered by the publication of *Silent Spring* by Carson (1962) and the various pro-environmental protest movements in the 1960s and 1970s (Guha, 2000; Zimmermann et al., 2001). It is now widely accepted that environmental questions are ethical questions. In order to understand the ethics of C&R, a brief sketch of these questions is also needed.

Human Beings, Nature, and Catch-and-Release

The traditional Western view of human beings is that they are the pinnacle of creation, and everything in it is entrusted to their care and use (Taylor, 1989; Aquinas, 1990; Calvin, 1990; van Wensveen, 2000). According to this view, human beings enjoy a special status in creation because they were created in God's image and through this enjoy intrinsic value; the source of that intrinsic value is divine. Intrinsic value, reason, and the capacity to generate moral knowledge and to live a moral culture make human beings unique in nature. Although all nature is related through creation, rocks, trees, or animals have no intrinsic value–at least not in the same sense as humans (Taylor, 1989; Aquinas, 1990; Calvin, 1990; van Wensveen, 2000). A tree, for example, is not a moral subject, but a moral object toward which a human being might have a moral obligation. This view allows for all kinds of interaction and intervention in nature because nature is created for human beings. Necessity apart, human beings are meant to interact, i.e., they are meant to participate actively in nature. The traditional Western view is labeled anthropocentric (Figure 1), and especially Christian anthropocentrism (there is also non-Christian, atheistic anthropocentrism, and biocentric anthropocentrism) is said to be responsible for what is perceived to be the current environmental crisis (White, 1995). The biblical sanction for use, according to the critics of Christian anthropocentrism, degrades nature to instrumental value only. This in turn is said to have bred an attitude of inconsiderateness toward nature which then resulted in the current situation (White, 1995).

Any sketch or treatise trying to portray the traditional Western view can and will be criticized by supporters and opponents alike on the grounds that it is either too sympathetic or too uncritical. Whatever the reasons for this situation, for the present purpose, it is important to note that the concept of "anthropocentrism" is not as clear as it might seem. In a relatively straightforward sense, it means "considering human beings to be the most significant entities of the universe" (Mish, 1993) or "regarding mankind as the center of existence" (Swannell, 1992). Murdy (1985, cited in Evans, 2005) defines anthropocentrism and draws attention to an interesting implication issue: "To be anthropocentric is to affirm that mankind is to be valued more highly than other living things in nature—by man. By the same logic, spiders are to be valued more highly than other things in nature—by spiders. It is proper for men to be anthropocentric and for spiders to be arachnocentric. This goes for all other living

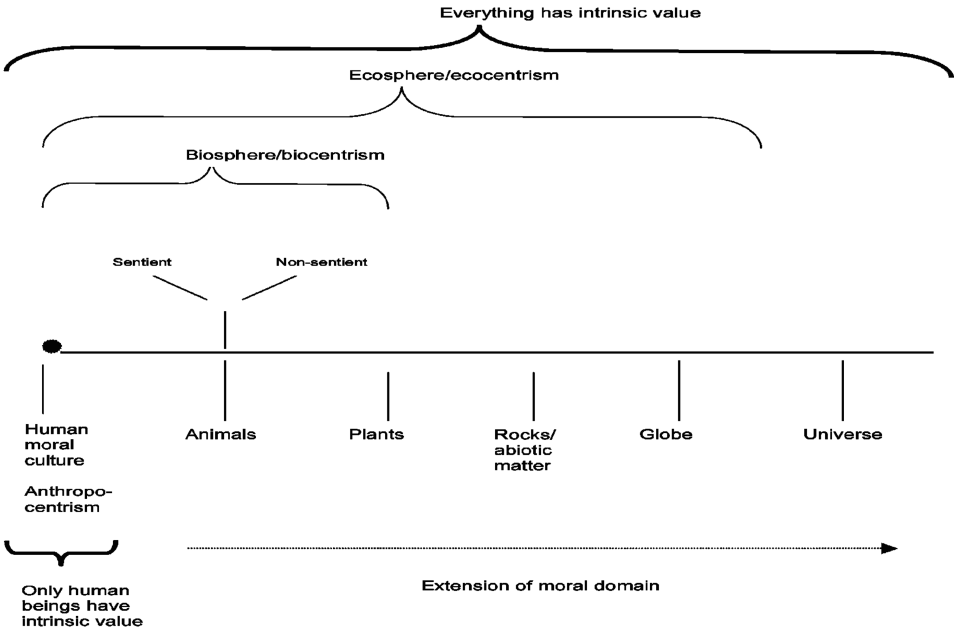

Figure 1. Schematic representation of the impacts of the extension of the moral domain from humans to non-human animals and abiotic matter as related to which components have intrinsic value that needs to be respected.

species." We use anthropocentrism loosely to cover all kinds of anthropocentrism, which is legitimate because all kinds of anthropocentrism share, regardless of philosophical content, the idea that somehow human beings are, at least for all practical purposes, in the center of reality, and, thus, the interests of humans to satisfy their needs comes first and everything else second.

A good example of anthropogenic reasoning, albeit not Christian anthropocentrism, is the definition of sustainability put forward by the Brundtland report (as cited in Arlinghaus et al., 2002): development is sustainable when it "meets the needs of the present generations without compromising the ability of future generations to meet their own needs." To avoid compromising the ability of future generations to meet their needs often involves avoiding environmental damage, i.e., nature and animals are not worthless, but of vital instrumental value to humanity as life support systems and generators of supporting, provisioning, regulating, and cultural ecological services (see Carpenter and Folke, 2006, for a review).

In contrast, physiocentric views, mostly based on or referring to the theory of evolution, regard the role and standing of human beings differently. For example, non-human components of nature such as animals are supposed to possess intrinsic value (Figure 1). All life is said to have begun in a primeval soup some time after the Big Bang. In this concoction, the first simple organisms formed and more complex life forms branched out. Then, somewhere along the line, the human species "happened." The advent of the human animal is seen as a pure random event in evolution, and human nature "is just one hodgepodge out of many conceivable" (Wilson, 2001). There is, from this angle, nothing special about mankind; "the species lacks any goal external to its own biological nature" (Wilson, 2001). If all life originated out of that primieval soup, all life is in some way related. This common evolutionary past and postulations like "reference for all life" or "respect for all life" have

given rise to concepts such that all life has intrinsic value and all animals are equal; this perspective has clear implications for C&R if this practice causes harm to animals.

The physiocentric evolutionary view has already changed common usage of words: it is nowadays practically standard to talk of animals not as animals but as non-human animals. Physiocentric views are almost always associated with the extension of the moral domain (Figure 1). The extension of the moral domain to the non-human world will, according to extensionists, bring about a different attitude to nature which will be the first step to solve the environmental crisis and also improve inter-human relationships (Naess, 1989; Merchant, 2003). Extensionist philosophers tend to be hostile to human intervention in nature because more often than not human influence on nature is seen as harmful. There is a discernible streak in much extensionist literature sketching an ideal of nature in terms of absence or minimal presence of human beings—that ideal is wilderness (Devall and Sessions, 1985; McKusick, 2000; Nash, 2001). Critics of the extensionist views point out that it makes little sense to extend the moral domain because the non-human world cannot in any way participate in the human moral or legal culture (Leahy, 1994; Scruton, 2000; Passmore, 2001).

The presumed presence or absence of intrinsic value and relative value of humans and animals (fish) shapes the cultural understanding of nature. What is held to be the nature of nature determines the guidelines of science, politics, and in the end, everyday life. The history and diversity of ideas and concepts about nature are rich and complete (Nash, 1989; Wall 1994; Teich et al., 1997; Guha, 2000; Foltz 2003), and a full discussion of them is beyond the scope of this article.

The word "nature" derives from the Latin *natura*, which has a range of meanings, including birth, shape, and essence, while culture stems from *cultura* meaning tillage and also education and training. In a wide sense, nature means the universe and everything in it, including an angler and his or her target, the fish.

In the anthropocentric sense, nature and culture are complementary opposites just like wilderness and civilization are complementary opposites. They are not mutually exclusive, but there is a mutual dependence and interaction between the human and non-human animal world. All beings are integral parts of nature, but it is clear that for an anthropocentric view, the needs of humans must come first, and in this sense nature is of instrumental value (Figure 1). Nature is a vital good for humans but also a good in itself and has to be protected for this reason. From an anthropocentric point of view, wilderness should be respected by humans for the emotional and practical good of humans, for reasons of conservation to preserve ecological services that indirectly benefit humans (e.g., to preserve the functioning of ecosystems and thus to preserve primary production, nutrient cycling, climate regulation, disease regulation, etc.), and for its own sake. This coincides with modern fisheries management thinking because fisheries management is defined as the use of all types of information (ecological, evolutionary, economic, political, and sociocultural) in decision-making that results in actions (e.g., regulations) to achieve human-defined goals established for fish resources (Arlinghaus et al., 2002). If C&R facilitates achievement of human goals established for fish resources and, provided that fish resources are respected and protected for meeting human goals and for conservation for their own sake, this practice does not necessarily conflict with anthropocentric world views.

Nature in the physiocentric account also means, in the widest sense, the universe and everything in it. In the narrower sense, however, there is, *a priori,* no license to use nature. The human's position in nature is at best *primus inter pares*, i.e., non-human species and plants and even abiotic matter have, in principle, the same rights as human beings, i.e., the right to live or be according to the specific requirements of their own nature. Human beings

also enjoy rights but must not infringe on the rights of another being or thing for purely instrumental reasons.

The spectrum and degree to which animals, plants, or even abiotic matter should be seen as right holders differs widely, of course. However, the common trait of all extensionist schools is the view that at least part of non-human nature is equal to the human animal as regards basic rights. The right of all beings and things or parts thereof to live according to their needs is the reason why wilderness is of such importance in extensionist philosophy. Wilderness is not a conceptual complement of civilization but a state in which all beings and things are in their proper natural balance. Some prominent extensionist philosophers hold that such a state indeed once existed in pre-agricultural stone-age societies (Oelschlaeger, 1991).

To complete this outline, eastern philosophies, especially Buddhism, Hinduism, and Taoism, play an increasingly important role in physiocentric thinking inasmuch as some influential thinkers stress the environmentally friendly nature of these philosophies (Snyder, 1995). C&R can seriously conflict with such physiocentric thinking if this practice compromises the rights of non-human animals and the proper balance of nature.

Regardless of origin, physiocentric thinking will tend to be in favor of the extension of the moral domain (Figure 1). This, however, does not necessarily preclude hunting, fishing, wildlife, or fishery management. Aldo Leopold, famous for his "Land Ethic" and its key phrase: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community" (Leopold, 1949), is an example of an extensionist who was an avid hunter and angler who occasionally also practiced C&R (Leopold, 1993).

Animal Welfare, Animal Liberation, and Animal Rights

The nature of the relationship of humans to nature as a whole determines our relationship to fish and other animals. Animal welfare, animal liberation, and animal rights concepts must be clearly distinguished because each of these concepts originates in a different philosophical tradition, and each of them has different implications for everyday life, the nature of our relationship with animals, for angling, and C&R (see Table 1 for summary).

Animal Welfare. Animal welfare is everywhere, broadly speaking, the notion that humans have a moral duty to care for animals, to prevent cruelty, and to look critically at how they are used (Dawkins, 2006). The crucial point is that the obligations animal welfare entails do not originate in the right of the animal (Table 1). The reason why this is so is the fact that animals cannot participate either in human moral or legal culture because they cannot fulfill obligations. The source of a moral duty is not necessarily a right on the part of the person, being, or thing to whom or which the duty is owed. It is, for example, everyone's duty to avoid wanton waste. The source of this duty is not a right of the waste not to be produced (Schwab, 2003). Or take the person who saves the runt of the litter from certain death by starvation: the moment the person starts feeding the little dog, there is an obligation to look after it, but that in no way signifies that the dog has a right. Compassion, moral sentiment, virtue, moral imperatives, contracts, common sense, customs, and even self-interest all can conceivably be the source of a moral obligation toward animals, but whatever the source of the obligation, animal welfare is a unilateral engagement in which animals have no rights proper and is based on anthropocentric world-views.

Animal Liberation. Singer (1990) is the author of the seminal book Animal Liberation. He is popularly and rightly hailed as the father of the animal rights movement, but Singer's

Table 1
Implications of animal welfare, animal liberation, and animal rights for the interaction of humans with fish

	Animal welfare	Animal liberation	Animal rights
Philosophical world view	Anthropocentrism	Physiocentrism	Physiocentrism
Fish have intrinsic value	No / Yes	No	Yes
Fish have rights	No	No	Yes
Duties to fish	Yes	Yes	Yes
Catch, kill, and eat	Yes	No	No
Regulatory catch-and-release	Yes	No	No
Voluntary catch-and-release	Yes	No	No
Recreational fishing	Yes	No	No
Fishery management	Yes	No	No
Use of animals (food, work, manufacture, pleasure, science)	Yes	No	No

theory has nothing at all to do with rights. "The language of rights," according to Singer, "is a convenient political shorthand" and "it is even more valuable in the era of thirty-second TV-News clips . . . " (Singer, 1990). Nevertheless we shall, in accordance with common usage, use the term "animal rights" to cover both the concept of animal liberation and the concept of animal rights unless, of course, there is a specific reference to either of the two. Singer's philosophy is a version of utilitarianism called preference utilitarianism. Utilitarianism defines morals in terms of consequences of actions, which is why utilitarianism is also called consequentalism. Actions "are right in proportion as they tend to promote happiness, wrong as they tend to produce the reverse of happiness. By happiness is intended pleasure, and the absence of pain; by unhappiness, pain and the privation of pleasure" (Mill, 1974, p. 257). Preference utilitarianism locates the moral good in the maximization of people's preferences.

Why animal liberation? Singer positions animal liberation in line with the liberation of slaves, the emancipation of women, and the end of prejudice against gays, lesbians, and all kinds of minority groups. Singer's message is that "animal liberation is human liberation, too" (Singer, 1990). Animals enter the moral theater because of a common evolutionary ancestry and because they are capable of suffering, i.e., pathocentrism-centered perspectives are the key to understand animal liberation. Suffering qualifies animals for equal consideration. Furthermore, the human animal must not be a speciesist. Speciesism "is a prejudice or attitude in favor of the interests of members of one's own species and against those members of other species" (Singer, 1990). Under the right circumstances, equal consideration and speciesism generate a duty not to use animals in any way. However, there are qualifications to this. If, for example, an animal does not suffer, we have no moral obligation to it at all. It ceases to exist, morally speaking. Another complication is that the maximization of preferences might lead quite to the contrary of animal liberation, namely that, for example, vivisection could be morally justified. It is also perfectly feasible that eating meat is under certain circumstances the right thing to do. There is just no telling for certain because it all depends on circumstances, i.e., the utilitarian calculus. How much happiness is produced by what set of preferences and which duties result from it can vary

dramatically. Nevertheless, on the strength of *Animal Liberation*, it is clear that recreational fishing and C&R are out of the question because, according to Singer (1990), there is no doubt that fish can suffer. This is clearly expressed by Singer (1990) in the following passage: "Surely, it is only because fish do not yelp or whimper in a way we can hear that otherwise decent people can think it a pleasant way of spending an afternoon to sit by the water dangling a hook while previously caught fish die slowly beside them."

Animal Rights. The name associated with animal rights is Regan and his book The Case for Animal Rights (Regan, 1983). Regan draws a distinction between moral agents and moral patients. Moral agents require a degree of self-consciousness and rationality so that they can understand the concepts involved in moral reasoning. Moral patients cannot perform moral acts themselves because their level of self-consciousness and rationality is insufficient to perform moral acts. Moral patients are on "the receiving end of the right and wrong acts of moral agents" (Regan, 1983). Examples of moral patients are animals or human babies that although self-aware to some degree do not qualify as moral agents. Moral agents and moral patients are, however, united in that "the principal moral right possessed by all moral agents and patients is the right to respectful treatment" (Regan, 1983). The source of this moral right is the postulate of inherent value (Regan, 1983). Inherent value does not come in degrees nor is it species-dependent: moral agents or patients cannot have more or less inherent value, and a dog, for example, has just as much inherent value as a rat, cockroach, or a child. As regards inherent value, all animals (human and non-human) are equal, and in consequence all moral considerations and actions must apply in the same way to all beings with inherent value. There are some ifs and buts in Regan's account, but in the final analysis, respect, our common evolutionary past (Regan, 1983, p. 19), and our position in nature (Regan, 1983, p. 388) make the human animal equal with all other animals. In practical terms, this means morally compulsory veganism and the end of all animal use everywhere regardless of consequence. It is clearly the end of any kind of recreational fishing including C&R (Table 1). There can be no misinterpretation of Regan on this. He is outspoken and unequivocal on the consequences of animal rights (Regan, 1983, p. 330–398).

Animal Welfare, Liberation, Rights, and Catch-and-Release

Sooner or later some of the philosophical considerations find their way into everyday life, which is what matters most for most people. On the strength of what has been outlined above, the implication is that C&R is, in principle, only acceptable under animal welfare philosophies. It is not acceptable if Singer's animal liberation and Regan's animal rights perspectives are taken for granted (Table 1).

The reality of social politics is different from an exposé. Politicians, sociologists, scientists, and a host of other people with an axe to grind invariably help themselves to ideas and arguments from the different schools and mix them into cocktails in which the individual ingredients are no longer distinguishable. It can, however, be documented that extensionism (e.g., animal liberation and animal rights), that is, the extension of the moral domain to non-human animals (Figure 1), has succeeded in changing laws and attitudes. In Germany and Switzerland, for example, the state has constitutional duties with regard to animals, and the not-yet-dead draft of the European constitution has a clause which specifies that the rights of animals must be taken into account by the European Union in all activities. In Germany, you must have a "reasonable reason" to inflict pain, suffering, and damage to an individual animal; typically, only fishing for food is acceptable as a good reason for angling overall (Arlinghaus, 2007). This has critical consequences for recreational fishing

in general, because C&R of unprotected fish risks public prosecution and imprisonment for up to three years, according to Clause 17 of the German Animal Protection Act (Arlinghaus, 2007). Many stakeholders may not see a good reason for a recreational activity that interacts with animals, particularly if labeled, and thus misinterpreted, as "sport" (compare the earlier discussion of origin of this word, deriving from "to disport"), which is often the case when speaking about extreme forms of C&R, i.e., total voluntary C&R or tournament fishing involving C&R.

In the present intellectual and political climate in Europe and the United States, all field "sports" will face some hard questions in the future. In Great Britain, the famous slogan "hunting, shooting, fishing" neatly summarizes the aims of the anti-field "sports" movement, which has its origin in animal rights philosophy. Rights for plants or rocks seem to be in the distant future, but philosophically speaking, they are already on the agenda. Talking about plants, Holmes Rolston, III, states "... plants too defend their lives. In an objective gestalt, some value is already present in non-sentient organisms, normative evaluative systems prior to the emergence of further dimensions of values with sentience. We agree with Singer that there is no feeling in such an organism, but it does not follow that humans cannot or should not develop 'a feeling for the organism' (Rolston, 1999)."

Suffering and Cruelty in Catch-and-Release Angling

The prominence of suffering, i.e., pathocentrism, as a central consideration in the relationship between human beings and animals is utilitarian in origin (Salt, 1980; Bentham, 1988; Singer, 1990). Suffering and speciesism are the pillars of the animal liberation philosophy. Suffering is also an important consideration in the animal rights view, but in the final analysis it is only rights that matter. Tom Regan is unequivocal. Human predation on animals in the form of hunting or fishing have to be banned "not out of kindness, nor because we are against cruelty, but out of respect for their rights" (Regan, 1983). Philosophically speaking, animal liberation and animal rights are worlds apart, yet their thrust is the same. Animal welfare is not doctrinal on suffering, but when it can be avoided, it should, or at least be minimized (Huntingford et al., 2006).

What precisely is a suffering fish? Suffering in animals is no more and no less difficult to define than it is in humans[3] and is dependent on consciousness, which is among the hardest aspects lacking understanding in contemporary biology (Dawkins, 1998). Huntingford et al. (2006) suggested that suffering is a more-or-less unpleasant mental or physical state felt by the animal. We chose to discuss this particular view of suffering because it is the most far reaching in consequence for recreational fishing and C&R. Mental or physical states mean the conscious experience of pain and fear of which the former takes prominence in angling-is-cruel debates. Can fish feel pain, experience fear, and, as a consequence, suffer?

Fish are different from humans. Their brain lacks, for example, the neocortex (Rose, 2002). In the human brain, the neocortex is involved in the conscious experience of pain, pleasure, fear, and other emotions. Emotional states require individuality or personhood, i.e., a single individual consciously experiencing a particular mental state. The absence of the neocortex suggests that the human experience cannot be like the fish experience and vice versa. There is, in a straight comparison, also no question of a sliding scale: the fish experience is not a scaled down human experience, nor is the human experience a scaled up fish experience. It could be reasonably argued that the absence of the relevant brain

[3]However, it is more difficult to *recognize* in other animals than in humans because humans can talk and tell us they are suffering, whereas other animals can only give nonverbal signals that must be interpreted by humans.

structure makes it impossible for fish to feel pain and experience suffering (Rose, 2002). The analysis of Rose (2002) seemed to confirm such a conclusion. However, other scientists have challenged his work. Sneddon et al. (2003), Chandroo et al. (2004), and Huntingford et al. (2006), among others, suggest the possibility that consciousness and pain perception in fish is plausible. Nevertheless, all of those authors acknowledge that the possible experience of fish is not anything near human experience. For example, Huntingford et al. (2006) venture that fish "probably have the capacity for suffering, though this may be different in degree and kind from the human experience." However, the human's ability to predict mental states in animals other than humans is likely to be very inaccurate because humans have not evolved the capacity to do so, i.e., for mind-reading (Marmeli and Bortolotti, 2006). By claiming that fish might suffer, Huntingford et al. (2006) as well as Chandroo et al. (2004) tacitly assume something that resembles or takes the place of the neocortex. This is not a question we can answer, but a challenge to provide conclusive evidence because of the implications of consciousness and the associated pain perception capability for angling in general and C&R in particular.

However, there is, among many stakeholders, laypeople, and scientists alike, the intuitive view that fish do feel pain and do suffer. The anthropomorphic reasoning is that the hook must hurt somehow. A typical representative of this view is Luce (1959), who thought that fish feel pain but that it would be "at a low degree of sensitivity." This intuitive common sense and empathic view resembles the position of Huntingford et al. (2006) and others such as Sneddon et al. (2003), mentioned above. Cruelty on the human side is the deliberate causing of suffering, and there is considerable academic and popular opinion that anglers do exactly that. Exemplary for this view is De Leeuw (1996) who, assuming that fish feel pain and suffering, puts it as follows: " . . . the enjoyment of catching fish for sport, in a large measure, consists of purposely inflicting fear, pain, and suffering on fish by forcing them to violently express their interest to stay alive." For the nature and definition of that interest, De Leeuw explicitly refers to Singer and Regan (De Leeuw, 1996). There is, nevertheless, a philosophical problem with this statement.

When an earthquake causes great suffering, we do not say the earthquake is cruel. It cannot be morally held responsible because it has no intention (List, 1997). Likewise, animals and plants have no intention in the moral sense because they lack the moral dimension. That is why there is no cruelty in nature. Cruelty is confined to human agency: humans can be cruel to humans, and humans can be cruel to animals (fish), provided the fish feel pain and suffering, for which there is no unequivocal scientific agreement. Cruelty in inter-human relations need not involve pain in a physical sense. There is suffering without physical pain, as in depression or a person's hurting another person with words. There is also (perceived) injustice, which can cause people to suffer for a lifetime. To an animal at the receiving end of an action that causes pain, the intention of the person performing that act does not matter. However, not all acts that involve the infliction of pain are cruel acts. Dentists, human doctors, and veterinarians often have to inflict pain in order to help. Whereas the human understands the intention, animals, as a rule, do not understand this, which is why they often try to flee when humans are trying to help them. In other words, the problem of cruelty is confined to human culture. This in turn means that the question of cruelty in fishing and elsewhere has an arbitrary component inasmuch as humans can decide on the scope of cruelty. Cruelty is not unambiguous like, say, a broken leg or a documented health impact or fitness impairment through C&R. This is why we prefer to avoid suffering in the fish welfare discussion and instead advocate focusing on health and fitness impairment resulting from C&R (Arlinghaus et al., 2007).

However, the intentional causing of suffering is, according to De Leeuw, the most important element for the enjoyment of fishing, and, on the basis of this, he concludes that "sport" fishing, including C&R, should be banned (De Leeuw, 1996). Similarly, Balon (2000) stated that "catching live fish on hook and line other than for food, i.e., for pleasure, leisure, "sport," or competition . . . is an unethical, deplorable, and undignified activity of humans." If De Leeuw's and Balon's arguments are deemed to be a valid basis for a ban on angling and C&R, some might argue that these arguments would also apply to cat keeping, because domestic cats kill or injure millions of birds and other wild animals. The following is quoted from De Leeuw (1996) and added in parentheses is the case against cat keepers: "The enjoyment of catching fish [keeping a cat] for sport [for pleasure]—consists of purposely inflicting fear, pain, and suffering on fish [birds] by forcing them to violently express their interest to stay alive." The argument would continue in that it could not possibly matter that the infliction of pain on birds is oblique. If one were to say that it is not the cat keeper's intention to cause suffering among birds, rodents, and amphibians, then that would also apply to the angler's intention. The angler's intention is not cruelty but to go fishing and maybe catch a fish (List, 1997).

In the passage above, the distinction is made between the intention to fish versus the intention to be cruel, but the issue in De Leeuw (1996) is that the intention of anglers is to do something directly to fish; it is not even theoretically possible to fish successfully without doing something to fish. In contrast, the intention of cat-keepers does not usually involve killing or harming birds, and it is possible in theory and in practice to keep a cat without harming birds (e.g., by keeping the cat indoors). However, each cat-keeper always risks that his or her cat injures or kills other animals if it escapes or is held outside; from the animal's perspective, the intention of the angler or the cat-keeper does not matter. Hence, it might be argued that the intention of humans to purposely inflict fear, pain, and suffering to an animal is as vague and subjective a concept as cruelty, as it does not tell us what type of impact occurs on animals directly (fishing) or indirectly (cat-keeping on birds).

The argument made in the previous two paragraphs is in the end useful because it demonstrates that reducing the fishing experience to largely one element does not correspond to what is the case. Fishing consists of a complex interplay of a multitude of motivations and needs that the angler wants to satisfy (Fedler and Ditton, 1994; Arlinghaus and Mehner, 2004) but very rarely involves cruelty as the goal of the activity (List, 1997; Schwab, 2003). Moroever, suffering of animals can occur indirectly in many, if not all, human activities even if it is not the intention of the human being; it is not unique to recreational fishing and C&R. Finally, the basis for judging the direct and indirect impacts of human activities on animals, including fish, can best be based on the level of impact on the animal's well-being irrespective of the human being's primary intention when deciding for or against certain actions. To assess potential impacts on fish in the context of C&R, it might be advisable to focus on objectively measurable indicators of fish health and fitness post release instead of relying on scientifically uncertain concepts such as suffering.

Implications for Catch-and-Release

Some forms of C&R could be seen as the perfect expression of the fact that recreational fishing is not about the necessity to obtain food. For example, for some voluntary C&R practitioners, to catch a fish is an end in itself. In such situations, there is no necessity or desire to kill and eat the fish; the voluntary C&R angler enjoys the full scope of the beauty and pleasure of angling, without the kill. As Browning (1998) noted: "For many fly fishers, killing a trout is unthinkable." However, there are ample variations in C&R behavior among

voluntary C&R practitioners; some release all the fish caught, others release a particular species or size, others release a fish or a particular species on one day but not on another day, and so on. For a voluntary C&R angler, the release itself is just as important as the catch, and for some anglers, the release is a little ritual, sometimes even begun by kissing the fish. The release is not just a perfunctory act, but has, for many, a spiritual dimension and, at the same time, is a manifestation of a consumption-critical and conservation-minded attitude. One could say, slightly overstating the case, that the gourmet catch-kill-eat angler is sent into raptures by his meal, while the C&R triggers a quasi-transcendental experience.

The idea that a fish is too valuable to be caught only once (Wulff, 1939) originated in the New World, and many in continental Europe have considerable difficulty coming to grips with the concept in purely intellectual terms. One of the reasons for the downright rejection or the lukewarm acceptance of the concept is the traditional equation, fish = food, i.e., subsistence fishing. This attitude has dominated the angling culture for centuries and is deeply engraved in the collective outlook. Perhaps the most lucid statement of this position is by Luce (1959): "The pleasures of angling explain why people angle; but the proper defense of the morality of our traditional sporting angling for game fish, and the angler's justification for taking life and inflicting pain, have nothing to do with the angler's pleasure. The defense and the justification are simply that the angler is killing fish for food." Moreover, by eating the fish, the entire process of fishing makes obvious sense. The angler participates in nature as a predator and acts accordingly, and regulatory C&R is part of the conservation of undersized or endangered fish. No ethical problem whatsoever is associated with this type of C&R for Luce and others (Håstein et al., 2005).

However, voluntary C&R is different. In voluntary C&R, one can perceive an anomaly because the angler breaks the normal behavior pattern of a predator or hunter. It is perhaps this anomaly that causes incomprehension. The days when food shortages and competition for food were the rule are not long ago; there might be some reflex that just wants to hold on to food. On the other hand, releasing the prey is not that extraordinary because acting in line with reason is a perfectly normal human behavior. C&R is after all not aimless and wanton as perhaps a fox who wreaks havoc in the henhouse, but a reasoned and rational approach to recreational fishing. All C&R, including voluntary C&R, also marches under the banner of conservation. The fish are put back to reproduce or to be caught another day, which also happens to be good news for the fishery manager. That sounds fine, but the same conservation results could also be achieved by cessation of fishing after the bag limit has been reached or by prolonged closed seasons. Conservation, it could be argued, is merely coincidental to C&R, whereas the nub of the matter is really that the angler wants to carry on catching fish. One could press even further and say that the C&R angler maximizes pleasure by exhausting, weakening, and mutilating fish, and by selling this, as it were, as conservation. We are full circle back to the issue of pain, suffering, and cruelty but with one added complication: the question of whether there are types of recreational fishing that are ethically different from other types of recreational fishing. Luce's view entails that there are, so to speak, morally inferior kinds of fishing and that C&R would be immoral.

However, C&R is an integral part of all angling. If, for example, an angler wants to catch perch (*Perca fluviatilis*) for his dinner, he or she will release the roach that is caught in pursuit of perch because the roach was bycatch. Furthermore, some of the perch the angler catches might be too small, so they are released. Some fish might not be well hooked and get away, which is "accidental" hook-and-release. To the fish, it does not matter whether it has been caught by a catch-and-kill angler, a C&R angler, or an osprey. All anglers accept, by the very act of fishing, that their activity can mean injury and death and perhaps pain and suffering to fish. All types of recreational fishing are open to, fundamentally, the same

charges, and these do not hinge on quantitative considerations. If it is not deemed acceptable that a fish "suffers" for time X, why should it be considered acceptable for time Y? If a fish suffers in C&R, it suffers in catch-kill-eat: both are either wrong or right. There is no divide in this respect between catch-and-kill and C&R.

With all the focus on human-induced suffering or injury, one tends to forget that suffering is not a human invention but rather a human experience. Suffering is one of the most basic facts of human life. Whether non-human animals experience suffering as a basic condition, as humans do, we cannot know for sure. Things in the animal world are without any consideration with regard to human-defined justice. However, human beings are, although in many respects special (language, reason, etc.), part of nature, and a sober view of nature is that it is red in tooth and claw. One could be tempted to say as Lockhart (1949) did "nature is cruel and man is its child." Nature is not cruel, but certainly man is its child. Human beings are predators, and, while it is true that that they are mainly emancipated from predation, out of necessity in many cases, there might still be an emotional need, an evolutionary disposition to hunt (Franklin, 2001); indeed, it is very likely that recreational fishing (like hunting) is very much an evolved behavior and thus may have a genetic component, like other activities that people find enjoyable (Orians, 1998) or choose to spend large amounts of time and money on (Dennett, 2006). Recreational fishing, including C&R, could thus be seen as a ritualized hunt that leads to experiences, which catch-and-kill does not generate (Evans, 2005). Evans (2005) went further by stating: "catch-and-release fishing can be a part of a practice that does give shape to our lives and to our relationship to the natural world . . . The practice of catch-and-release fishing is most properly based on respect for the integrity of ecosystems and populations that are subjected to the pressures of human use and exploitation. Embedded in this practice is a specific respect for the individual fish one attempts to catch and then release. This respect is embodied in the constraints that the intent to release the fish puts on the methods and tackle used."

Conclusion

To go fishing means to actively participate in and appreciate nature. Only through participation can human beings see, for example, the beauty and variety of life in nature and thereby learn to respect it (Schwab, 2004; Evans, 2005). All big Eastern and Western cultural traditions allow or allowed the use of animals (Benecke, 1994). Human beings are not meant to step apart from nature, nor can they stop interaction with wildlife. In recreational fishing, humans act in nature as predators capturing fish. As it happens, they enjoy themselves doing so and, more importantly, often reflect about what they are doing. The pleasure of angling is a pleasure in nature, and the experience involves psychological, social, aesthetic, physical, culinary, scientific, philosophic, spiritual, and many more aspects, all of which can be the source of pleasure. Pleasure is good for humans and for their well-being. Human beings need pleasure, and the most natural source of pleasure is nature (Franklin, 2001; Schwab, 2004). From most anglers' point of view, these are sufficient reasons to justify C&R fishing.

It could be argued that there are other sources of pleasure in nature that do not involve playing around with one's fellow animals, e.g., watercolor painting. Angling and C&R, according to this rationale, are not necessities. But necessity is not really an argument: you can behead anything with it. You can randomly take any activity or object and question its necessity and arrive at the conclusion that the activity or thing in question is not a necessity. Watercolor painting is not a necessity either, and in the activity a great many animals and plants suffer. Suppose the painter wants to paint a landscape and selects an elevated spot

with a beautiful view. In order to get there he has to walk across country, trampling on many animals and plants, intentionally or unintentionally killing and destroying some of them. When putting up the easel, he does likewise, and what about the colors, canvass, and tools (the best water color brushes are "natural") he uses? The production, transportation, and distribution of these items are potentially environmentally unfriendly and probably violate some being's rights. Or consider the mushroom hunter: in trampling over dead leaves, he kills and mutilates tiny animals. Moreover, is his mushrooming necessary? Take horse riding and horse racing: are they a necessity, and do they not cause a lot of suffering? Take hill walking, take any pursuit in nature, and, on closer examination, you could construe all human interaction with nature as potentially harmful and as causing suffering and injury of a kind.

The point is that humans are part of nature, and nature is the environment in which they must survive but also the environment in which they find pleasure. To deny humans pleasure in nature is to separate them from it, precisely for which many prominent extensionist philosophers argue. J. Claude Evans puts it succinctly: "Rejecting the idea that the natural world exists as a pure resource for human use, many argue that human beings are obligated, to the greatest extent possible, to refrain from using nature as a resource at all. The result is a curious mirror image of anthropocentrism, as human beings are once again removed from nature. But this time the removal goes in the opposite direction from that taken by anthropocentrism. Instead of the removal making us the lords of nature that exists for our use, this new removal involves the moral obligation to take ourselves out of participation in natural processes, to the greatest extent possible, out of respect for nature" (Evans, 2005).

Many forms of contemporary environmentalism and animal rights aim at radically reconstructing society in harmony with nature and along cruelty-free lines. There is no room for paddling in such a world of thought. If paddling is wrong, all recreational angling and all C&R is wrong. In pressured waters, this perspective can conflict with the traditional goals of fishery management and fish conservation, which aim at protecting fish and fish populations and aquatic ecosystems for their own sake, for reasons of conservation, and, at the same time, for the emotional and practical good of human beings. In this respect, C&R, either mandated or voluntary, can be viewed by managers and anglers as a viable complement to catch-and-kill recreational fishing. As long as stakeholders work for increased welfare status of fish during and after the C&R event, this perspective is in agreement with animal welfare perspectives as discussed in this article and summarized in Table 1. In contrast, animal liberation and animal rights ideas do not tolerate any interaction with fish, which necessarily translates into a ban on recreational fishing and C&R. The German example also shows that an intermediate way can develop in which subsistence-like recreational fishing is tolerated, mandated C&R of protected fish species and sizes is accepted, and voluntary C&R of unprotected fish is, implicitly, forbidden (Arlinghaus, 2007).

Social change will dictate the future of C&R, indeed, of recreational fishing in general, in different jurisdictions and cultures around the world, and these developments will most probably be based on the ethical concepts discussed above. Fisheries managers and other stakeholders are well-advised to pay attention to these developments because of their implications for fisheries management and the way angling can be conducted.

Human Dimensions of Catch-and-Release

After iterating that history, culture, and ethics are paramount to understanding how the angler and non-angler approach and view C&R, we now turn to a review of social and psychological studies that have examined C&R behaviors or behavioral antecedents (e.g.,

attitudes) of anglers. Until recently, relatively little effort has been directed at understanding anglers who practice C&R and why they choose to do so. Consequently, C&R is often used as a management tool with little understanding of how such regulations are likely to be accepted by anglers (e.g., Matlock et al., 1988; Ditton and Fedler, 1989; Payton and Gigliotti, 1989). Agencies and other organizations promote voluntary C&R with little understanding or consideration of the processes through which innovations such as these are adopted and diffused throughout the angler population (Rogers, 1983). Most educational and promotional efforts have used broad messages and catchy slogans, with the apparent assumption that most anglers will be receptive to such efforts and will be encouraged to change their behavior accordingly. Moreover, many fisheries managers and anglers appear to see C&R as the solution to many of the problems of sustainability facing recreational fisheries. This apparently simplistic view does not recognize the diversity within angler populations in terms of attitudes, motives, preferences, and satisfactions, which will likely result in a large amount of variation among anglers in the extent to which C&R is understood, accepted, and practiced.

As C&R fishing becomes a more integral part of recreational fisheries worldwide, there is a growing need to understand anglers who choose to participate in this type of fishing. From a multiple-satisfactions approach to fisheries management (Hendee, 1974), this information is crucial for ensuring that the needs and desires of these anglers are met. Traditional management efforts that focus on maximizing size or number of fish harvested will not be sufficient to provide all of the opportunities and experiences desired by this growing non-traditional angler segment. Moreover, if agencies want to promote increased participation in C&R, promote best-practice release techniques, and use C&R as a management tool or as a means of collecting biological data (e.g., through angler-based fish tagging studies), they must understand current attitudes and behaviors and be able to target effective communication toward those anglers who are most likely to be receptive. Although the success of C&R meeting these management goals will depend on the level to which it is adopted and practiced correctly by anglers, there has been surprisingly little research on the human dimensions of C&R compared to the number of studies that focus on the effects of C&R on fish and fish populations.

Catch-and-Release and Angler Specialization

The concept of recreation specialization provides a framework whereby we can begin to predict which anglers are likely to be receptive to the C&R philosophy. Recreation specialization was proposed by Bryan (1977) as a means of exploring the diversity of recreationists participating in an activity. The concept of specialization suggests that anglers can be arranged along a continuum, ranging from novice to specialist, depending on their avidity and experience, fishing preferences, orientation to the fishery, and the importance of fishing to their lifestyle (Bryan 1977). Bryan (1977) suggested that, as one's level of specialization increases over time, focus shifts from consumption of the fish to preservation, and greater emphasis is placed on the nature and setting of the activity. For the most specialized anglers, the object of angling shifts from the fish to the experience of fishing as an end in itself (Bryan 1977). Bryan (1977) was the first to propose that highly specialized anglers would be more supportive of C&R policies to maintain healthy fish populations.

Subsequent studies of various angler populations and sub-populations have confirmed that more specialized anglers tend to be less consumptively oriented, more likely to practice C&R, and more likely to support catch-and-release regulations (Gigliotti and Payton, 1993; Fisher, 1997; Chipman and Helfrich, 1988; Allen and Miranda, 1996; Quinn, 1996;

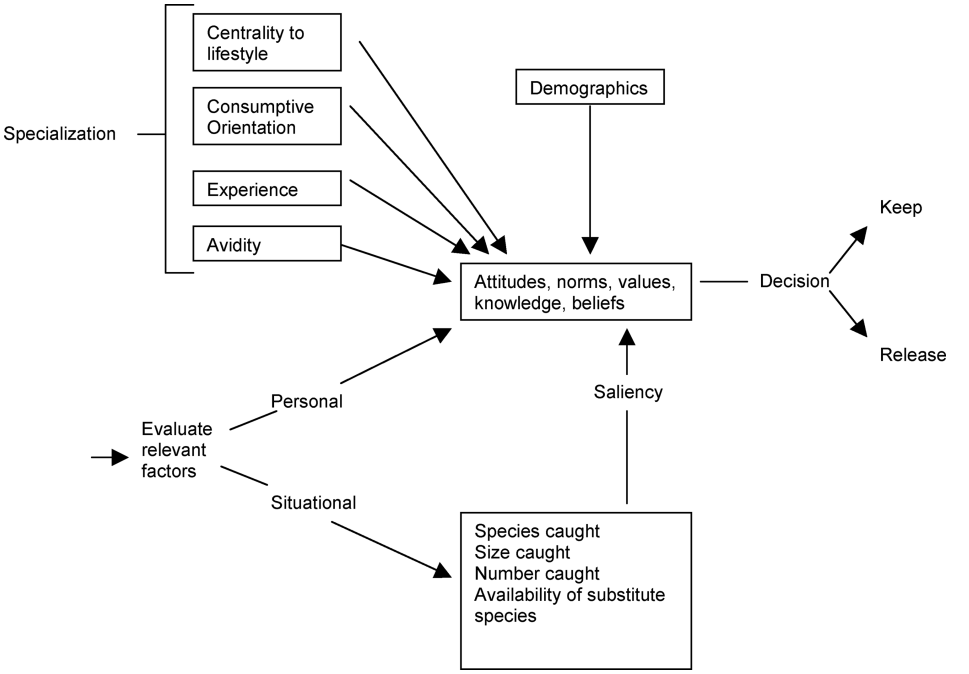

Figure 2. Conceptual model of variables determining voluntary catch-and-release behavior of anglers.

Margenau and Petchenik, 2004; Arlinghaus and Mehner, 2003; Salz and Loomis, 2005). Whereas these studies have been useful for segmenting angler populations and identifying which segments are more receptive to the C&R philosophy, they have not been very useful for identifying the underlying predictors of C&R attitudes and behavior. Sutton and Ditton (2001) recommended that future research should focus on the underlying dimensions of specialization (e.g., commitment and consumptive orientation), which would be most likely to influence C&R attitudes and behavior (Figure 2).

Catch-and-Release from a Human Dimensions Perspective

Researchers interested in C&R from a human dimensions perspective have used differing definitions of C&R (Ditton, 2002). Grambsch and Fisher (1991) classified C&R anglers as those who reported voluntarily releasing any of their catch (on a species-specific basis) for any reason at any time over the previous twelve months. Whereas this classification is useful for discriminating anglers who never practice voluntary C&R from those with a propensity to do so, it provides little insight into the factors that influence C&R behavior. Graefe and Ditton (1997) classified C&R billfish anglers as those who voluntarily released all of their billfish catch over a 12-month period, and Aas et al. (2002) defined "C&R fishing" as angling where all fish caught are released. These definitions allow research to focus on understanding the characteristics of anglers who always release all of their catch (or all of their catch of a single species); however, these definitions provide no information about anglers who practice C&R some of the time and why they choose to release fish in some situations and not others.

Fedler (2002) used responses to five statements concerning harvesting and releasing fish to create a harvest-release scale that classified anglers as harvest-oriented, harvest-and-release-oriented, or release-oriented. This classification allows for greater separation and understanding of anglers based on the extent to which they participate in voluntary C&R; however, like other classifications, it provides no information about how and why anglers decide to keep or release caught fish.

Sutton (2001) provided a more comprehensive definition of C&R behavior that was aimed at facilitating further human dimensions research and conceptual development in this area. In that study, C&R was defined as a specific behavior (i.e., live release of an angled fish) that is under volitional control of the angler. Under this definition, an angler's choice to participate in C&R can be made at the time the fish is caught or prior to engaging in the fishing activity. Thus, an angler who releases an undersized (non-legal) fish is not practicing C&R (from a human behavior perspective) because behavior in that situation is constrained by regulations (the angler could choose to disobey the regulations, but that would be considered a different behavior). However, an angler who catches (and releases) fish in an area designated "C&R only" is practicing C&R because a choice to release caught fish would have been made prior to engaging in the fishing activity at that location. This definition of C&R as a specific behavior that the angler must choose to perform is consistent with operationalizations of behavior used by social psychologists (Ajzen and Fishbein, 1980). Sutton (2001) suggested that treating C&R in this way allows research to focus on the factors that influence the choice of whether or not to practice C&R in any given situation as well as the factors that influence the relative frequency with which C&R is practiced over a given period of time.

Explaining Catch-and-Release Behavior

Early studies on the human dimensions of C&R were largely atheoretical and descriptive. Grambsch and Fisher (1991) provided participation rates in C&R for various subgroups of black bass and trout anglers in the United States. Overall, they found significant positive correlations between C&R participation and household income, education level, fishing frequency, and number of fish caught in a one-year period. Graefe and Ditton (1997) examined predictors of C&R behavior of billfish tournament anglers. They found a significant negative relationship between the probability of releasing all billfish caught during a 12-month period and the number of billfish fishing trips taken over the 12 months, the number of tournaments entered over a 12-month period, and income. These studies suggest that demographic and behavioral variables may be useful for predicting which anglers are likely to practice C&R (Figure 2) but provided little insight into the factors that influence anglers' decisions to release caught fish.

Fedler (2002) classified saltwater anglers in Maryland as either harvest-oriented (43%), harvest-and-release oriented (33%), or release-oriented (24%), and investigated differences in responses to motivational and management-related statements between the groups. Harvest-oriented anglers rated motivational statements "to obtain fish for eating" and "to catch my limit" significantly higher and placed more importance on the fishing location attributes of being able to catch the preferred type of fish and catch a limit of fish than did other anglers. Conversely, release-oriented anglers showed stronger support for fishery management alternatives that affected the number and size of fish caught, when and how fish could be caught, and where fish could be caught. Fedler (2002) concluded that the results indicate that the basic difference between harvest-oriented and release-oriented anglers lies in their consumptive orientation.

Sutton (2001) took a more theoretical approach to understanding C&R behavior. He developed a theoretical framework to understand the choice to release caught fish based on previous research and theory in the fields of outdoor recreation and social psychology. The theoretical framework (Figure 2) assumes that an angler's decision to keep or release caught fish is arrived at through a rational process in which all relevant personal and situational factors are evaluated. The immediate determinants of the choice to release caught fish in any given situation are thought to be the individual's attitudes, beliefs, values, knowledge, and norms, which in turn are hypothesized to be a function of the angler's level of commitment to fishing (i.e., the degree to which an individual has become behaviorally and psychologically bound to the activity [Buchanan, 1985]) and the angler's consumptive orientation (i.e., the importance the angler places on the catch-related outcomes of the fishing experience [Fedler and Ditton, 1986]). Situational factors are attributes of the situation in which the decision to keep or release caught fish takes place (e.g., size and species of fish caught, social group fished with). Situational factors are hypothesized to affect the C&R decision by influencing the saliency of the angler's beliefs, attitudes, values, knowledge, and norms. The effects of personal and situational variables on C&R behavior were tested in a series of studies with bluefin tuna, *Thunus thynnus*, in North Carolina (Sutton and Ditton, 2001); billfish anglers in Mexico and Costa Rica (Sutton, 2001); and bass, crappie, and catfish anglers in Texas (Sutton, 2003).

Personal Variables. Sutton (2001) proposed that more committed anglers (i.e., anglers who are more experienced and anglers for whom fishing is a central part of their lifestyle) should be more receptive to the C&R philosophy and more likely to practice C&R. Committed fishers should be highly dependent on fishing to meet their leisure and social-psychological needs and therefore more likely to view C&R as a way to ensure that fishing opportunities are available in the future (Sutton and Ditton, 2001). Centrality to lifestyle was found to be a significant predictor of participation in C&R for Atlantic bluefin tuna anglers (Sutton and Ditton, 2001) and billfish anglers in Mexico and Costa Rica (Sutton, 2001). However, centrality to lifestyle was not found to be a predictor of C&R choice for freshwater (bass, crappie, and catfish) anglers in Texas (Sutton, 2001, 2003). Sutton (2001) suggested that bluefin tuna and billfish anglers, for whom fishing constitutes a high centrality in their lifestyle, may see a greater need to practice C&R as a way to ensure future fishing opportunities for these species (which have well-publicized conservation issues) than do anglers who target freshwater species in Texas (where fish populations are generally not considered depleted and are often maintained or augmented through stocking programs). Level of previous experience was not found to be a significant predictor of C&R behavior in any of the angler populations studied (Sutton and Ditton, 2001; Sutton, 2001, 2003). Sutton and Ditton (2001) suggested that previous experience may be important only to the extent that it allows angling to become a central part of the angler's lifestyle; once this attachment to fishing is established, level of previous experience appears to have little influence on the decision to keep or release caught fish.

An angler's consumptive orientation (Fedler and Ditton, 1986) has also been hypothesized to influence C&R behavior (Sutton, 2001; Sutton and Ditton, 2001; Sutton, 2003). The concept of consumptive orientation recognizes that pursuing, catching, and retaining fish may be most important for some anglers, whereas, for other anglers, fishing may be a means of attaining other experiences from which satisfaction is derived (Hendee, 1974; Hampton and Lackey, 1975; Driver and Cooksey, 1977; Fedler and Ditton, 1994). Sutton (2001) suggested that anglers who place low importance on the catch-related aspects of fishing should be more likely to practice C&R because satisfaction for these anglers is not

highly dependent on catching or keeping fish (Vaske et al., 1982, but see Arlinghaus, 2006, for contradictory results) and may even be enhanced by releasing caught fish.

A number of studies have examined the influence of four catch-related aspects on C&R behavior: 1) importance placed on catching "something", 2) importance placed on keeping fish, 3) importance placed on catching a trophy fish, and 4) importance placed on number of fish caught. Only importance placed on keeping fish has consistently been found to have a strong negative effect on C&R behavior (Sutton and Ditton, 2001; Sutton, 2001, 2003).

Whereas some anglers may place low importance on number of fish caught, catching "something," or catching a trophy fish, this apparently does not influence C&R behavior, probably because these dimensions tap into attitudes that are largely unrelated to keeping or releasing fish. Consequently, anglers who are classified as "low consumptive," because they place low importance on one or more of these three dimensions, will not necessarily harvest fewer fish than anglers classified as "high consumptive," nor will they necessarily be more likely to support increased use of C&R as a management tool. Arlinghaus (2006) showed for German anglers that the assumption that low catch-oriented anglers are less dependent on catching fish for deriving satisfaction may not be valid, because all anglers irrespective of self-reported level of catch orientation derive most of their satisfaction from catch-related aspects of the fishing experience.

Situational Variables. Sutton (2001) suggested that situational factors may influence C&R behavior by influencing the beliefs, attitudes, and norms that are brought to bear on the C&R decision. For example, whether an angler believes that releasing a caught fish is a waste of food may depend on the size or species of fish caught or the number of fish already retained on that trip. A number of studies have provided evidence that situational variables play an important role in determining whether an angler keeps or releases a caught fish. In an early study of C&R participation rates for bass and trout anglers, Grambsh and Fisher (1991) reported that the primary reason anglers voluntarily released caught fish was that the fish were "legal to keep, but too small," suggesting that size of fish caught may be important in determining attitude toward C&R in any given situation. In a study of bluefin tuna anglers, Sutton and Ditton (2001) found that two of four situational variables tested (number of tuna caught and fishing party size) significantly influenced anglers' decisions to keep a bluefin tuna, even after controlling for the effects of personal factors.

Sutton (2003) used a series of hypothetical scenarios to test the effects of size and species of fish caught (in conjunction with personal variables) on the C&R decisions of freshwater anglers in Texas. When personal and situational variables were included in a single model, the odds of choosing to release a caught fish varied according to species caught and whether the species was the angler's preferred species, as well as the personal variables importance placed on keeping fish and species preference. Results also showed that anglers were more likely to release small fish than large fish, but anglers who placed high importance on catching a trophy fish were significantly less likely to release larger fish than smaller fish, indicating that personal and situational variables can have interactive effects on the C&R choice.

An unrelated study provided additional support for the hypothesis that situational variables affect anglers' decisions to release (or keep) caught fish. In a study designed to understand the fish harvesting behavior of walleye, northern pike, and smallmouth bass (*Micropterus dolomieu*) anglers, Hunt et al. (2002) found that the number of fish caught was one of the most important determinants of anglers' decisions to retain caught fish (anglers released a higher proportion of caught fish when catch rates were high). Results of that study also showed that retention rates for northern pike and smallmouth bass were

related to the catch rates of substitute species (i.e., when catch rates of the target species were low, high catch rates for substitute species had a negative effect on the retention rates of the target species). Importantly, the study by Hunt et al. (2002) also found that, whereas the importance placed on catch-related motivations influenced fish harvesting behavior, the explanatory power of the catch-related motivations was considerably weaker than the influence of situational factors.

Conclusion. Research reviewed above supports the general theoretical framework developed by Sutton (2001), in which C&R choice is hypothesized to be a function of both personal and situational variables. In particular, importance placed on keeping fish, centrality to lifestyle, and size and species of fish caught appear to be important determinants of the C&R decision for many anglers. Significant interactions observed between and among personal and situational variables indicate that these variables do not always operate independently of each other. Results of previous studies also suggest that determinants of the C&R choice may vary somewhat across angler sub-populations. To date, the range of personal and situational variables examined has been narrow, and only a small number of angler sub-populations have been studied. Consequently, it is likely that important determinants of C&R behavior remain unidentified.

Beliefs and Practices Regarding Catch-and-Release and Released Fish Survival

Few studies have directly questioned anglers about their C&R beliefs and practices or about their willingness to adopt practices that increase the survival of released fish. One comprehensive study conducted in Australia, however, has addressed some of these issues. As part of a national strategy to promote the survival of released line-caught fish, an Australia-wide survey was conducted in 2002 to understand anglers' perceptions and practices regarding C&R (Roy Morgan Research, 2003). The survey was followed by a national television campaign to promote best practices in releasing line-caught fish; a subsequent survey was conducted in 2004 to assess the effectiveness of the campaign (Roy Morgan Research, 2004). In the initial survey, 88% of active anglers reported releasing fish. for any reason, over the previous two years; 76% reported voluntarily releasing fish during that time. Anglers who reported releasing fish over the previous two years were asked to rate their level of agreement with a series of statements related to their C&R beliefs and behaviors. Results are summarized in Table 2. Overall, most anglers believed that they know the correct release techniques and have the correct equipment for releasing fish, that most released fish survive, and that there are benefits to themselves and to fish populations in releasing caught fish. In addition, 66% of anglers reported that they were aware of practices that should be used when releasing fish. Forty-eight percent of anglers said they would be inclined to use new fishing gear that improves released fish survival if it makes no difference to catch rates; 25% said they would use new gear that improves survival even if it reduced their catch rate (Roy Morgan Research, 2003).

Anglers were also asked about their perceptions regarding C&R practices. A majority of all anglers believed that fish survival could be increased by: holding fish gently in the water (92%), using barbless hooks (79%), using a landing net (76%), playing fish hard to land them quickly (65%), using wet hands to handle fish (65%), and cutting the line to leave deep hooks in fish (59%). A majority of anglers believed that fish survival would be decreased by: holding fish out of water for several minutes (94%), using a gaff to land fish (82%), holding fish vertically by the jaw (57%), and removing deep hooks with a "hookout" or pliers (51%). Additionally, 45% of anglers believed that using lures or flies in preference

Table 2
Australian anglers' level of agreement with statements related to catch-and-release

	Level of agreement (%)		
	Agree	Neutral	Disagree
I don't see any benefit to me in releasing the fish I catch.	8	4	88
I believe that released fish benefit the fish stock.	95	3	2
I believe that most released fish die.	6	7	87
It is more satisfying to me to release fish rather than keep them.	49	22	29
I don't need to keep all the fish I catch to have a successful fishing trip.	90	2	8
I don't have the equipment to properly release fish.	11	6	83
I don't know the proper catch-and-release techniques.	22	6	72

to bait made no difference to released fish survival, and 35% believed that deflating the swim bladder of fish caught in deep water decreased fish survival (23% believed this technique increased survival). Sixty-two percent of anglers did not know what a circle hook was (Roy Morgan Research, 2003).

The follow-up survey conducted after the television campaign designed to promote best practices in releasing fish found that 59% of anglers were aware of the campaign and recalled at least one aspect of it. Eighty-three percent of anglers who recalled the campaign (49% of all anglers) said that the information provided was somewhat or very effective at encouraging them to change their fishing/releasing practices, and 35% of all anglers reported actually changing their fishing/releasing practices in response to information provided by the campaign (Roy Morgan Research, 2004). These results suggest that educational campaigns can be effective at changing the C&R practices of some anglers.

Conclusion

Many fisheries management agencies and non-governmental organizations are interested in promoting C&R as a means of reducing harvest from recreational fisheries resources, allowing more anglers to have access to quality fishing opportunities, and ensuring the sustainability of recreational fishing. The success of C&R in meeting these objectives will depend on a sufficient number of anglers adopting the behavior and practicing proper release techniques. The research reviewed here suggests that there will be variation in the extent to which anglers adopt and practice C&R and that the reasons why anglers choose to keep or release caught fish are diverse and complex.

Biological Aspects of Catch-and-Release

The biological aspects are probably the most studied component of C&R angling and are better understood than the human dimension of C&R. However, even with several hundred papers and earlier syntheses (Muoneke and Childress, 1994; Policansky, 2002; Bartholomew and Bohnsack, 2005), there are still many questions that remain unanswered and many species and fisheries for which there is negligible information on mortality or

other sublethal consequences of angling (Cooke and Suski, 2005). None of the earlier syntheses (i.e., Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005) have given a comprehensive review of all available literature or the biological aspects of C&R angling, and there has especially been little focus on non-lethal (i.e., sublethal) and population effects. Here we summarize the available literature on the biological consequences of C&R angling on freshwater and marine fishes. For our qualitative review, we focus on literature and aspects that have not been included in previous syntheses. We have made a special effort to include new literature, cover different geographical areas, and emphasize sublethal effects. Collectively, this synthesis will provide the reader with the state of knowledge of biological aspects of C&R, help to identify measures to reduce the negative biological consequences of C&R, and identify future research avenues.

One way to consider the biological effects of C&R angling is to develop a qualitative model that describes the suite of possible factors that mediate the presence or magnitude of different biological endpoints (see Figure 3 for a simplified schematic for a C&R angling event). For this discussion, an "endpoint" is any biological effect arising from C&R angling activity. These effects can be as fine-scale as at the level of the cell or be as broad as effects at the population level. A typical C&R angling event includes a number of factors (herein called explanatory variables) that determine the presence or magnitude of different endpoints. In this review, we summarize how C&R angling affects different endpoints and how these endpoints have been or could be used in the study of C&R effects. In addition, we present the explanatory factors that contribute to the different biological endpoints identified before. Finally, we summarize C&R angling endpoints and explanatory variables using a quantitative literature review that covers most of the available literature since 1957 to evaluate temporal trends in C&R research activity across the world.

Catch-and-Release Angling Endpoints

C&R angling has the potential to negatively affect or alter almost all biological processes which contribute to survival and an organism's role in the community (Cooke and Sneddon, in press). At the extreme is mortality, where an organism dies from C&R related effects–usually injury, stress, or a combination of those factors. When considering biological effects, it can be instructive to summarize the generalized stress response. For example, at the primary level (e.g., endocrine system), there begin a number of cascades that control how an organism responds to a stressor. At the secondary level, a number of biochemical and organ level (e.g., metabolites, changes in organ systems such as cardiac activity) alterations occur in response to the cascade initiated at the primary level. Finally, at the tertiary level, responses become evident at the organismal level (e.g., whole-animal), where effects can occur on growth, migratory behavior, and fitness. These effects can also be extended beyond to include effects at higher levels of biological organization such as the population, community, or ecosystem. For purposes of this synthesis, we break down these endpoints into seven logical components, including terminal (i.e., mortality/predation) and sublethal endpoints (i.e., injury, stress, behavior, fitness/reproduction, growth/energetics, and population/ecosystems). Below we summarize each endpoint and describe the basic mechanisms underlying it. We also evaluate how the endpoint relates to C&R angling including its relevance and how it is used in the assessment of C&R angling impacts. In a general sense, we are interested in distilling this information down to understanding the range of factors that contribute to a given endpoint. In later sections, we explore those factors in more depth.

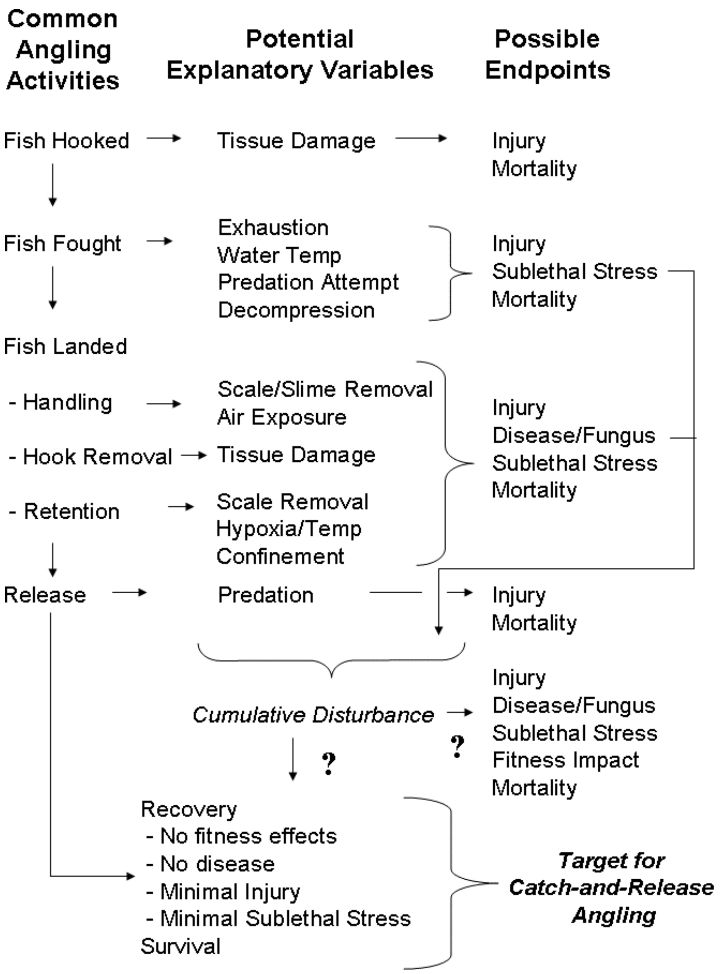

Figure 3. Simplified schematic of some of the primary factors that affect catch-and-release endpoints from a biological perspective. This schematic is generalized and could be adapted for a specific fish, environment, or fishery. Question marks indicate improper gaps of knowledge.

Terminal Endpoints

1. Mortality. The widespread adoption of C&R is predicated on the general assumption that released fish will survive (Wydoski, 1977). Because most fish that die from C&R angling do not die immediately after release (Muoneke and Childress, 1994), the presumption is that mortality is negligible. However, using a combination of holding and tagging studies, it has become clear that mortality can in fact be quite high. For example, Muoneke and Childress (1994) reported that mortality rates for released fish ranged from 0–89% across a variety of marine and freshwater species. A more recent synthesis by Bartholomew and Bohnsack (2005) revealed that mortality rates were still high for many species despite greater knowledge (relative to Muoneke and Childress, 1994) of the factors that contribute to mortality. Hooking mortality is usually divided into immediate or initial mortality and delayed mortality. Immediate or initial mortality is defined as capture-related death that occurs during and following capture, up to the time the fish is released. Delayed mortality

represents death from C&R angling at some point after the released fish swims away. Delayed mortality is usually determined by holding fish in cages, pens, or hatchery ponds, or by affixing transmitters/tags to them. Total hooking mortality is the sum of initial and delayed mortality minus the cross-product of initial and delayed mortality (Wilde et al., 2003a). Muoneke and Childress (1994) reviewed studies on hooking mortality in both marine and freshwater fish and suggested that total hooking mortality rates above 20% should generally be considered unacceptably high. In recent years, it has become apparent that controls are important when attempting to derive true estimates of C&R angling mortality. Control fish should be captured using other techniques (e.g., netting, electrofishing) and should quantify any negative consequences of retention or general handling.

2. Predation. The ability to avoid and evade predators is based on being able to sense the predator and then respond appropriately. There is clear evidence that stress causes significant deficits in predator avoidance and evasion (Schreck et al., 1997). Fish may be vulnerable to predation immediately after C&R angling due to short-term stress effects and physiological constraints resulting from exhaustion, but also by being released in an area where they do not normally reside (in open water, out of their school, away from shelter, etc.). Predators may also be attracted by the noise and movements during the angling and release event, or by olfactory or other stimuli from a stressed and injured fish (Smith, 1992; Bleckmann and Hofmann, 1999). Fish brought from greater depths may have problems maintaining equilibrium after release and getting back to deep water due to depressurization/decompression (see depth section below), which may further increase predation risk.

Only one study explicitly covers predation after C&R angling (Cooke and Philipp, 2004). In that study, a high mortality (39%) of bonefish, *Albula* spp., was recorded in high shark abundance areas as a direct result of predation within 30 min after release, whereas no mortality was recorded in low shark abundance areas. Other authors report anecdotal observations of predation, probably as a result of C&R, by sharks (e.g., predation on Atlantic sailfish, *Istiophorus platypterus* [Jolley and Irby, 1979]; predation on tarpon, *Megalops atlanticus* [Edwards, 1998]), marine mammals (e.g., bottlenose dolphin predation on red snapper, *Lutjanus campechanus* [Burns et al., 2004]), and predatory birds (predation on cichlids [Thorstad et al., 2004]). In a study of survival of released sub-legal cod, *Gadus morhua*, caught in the longline fishery, observations of predation by sea birds were also reported (Milliken et al., 1999). For species providing parental care by nest-guarding, such as smallmouth bass and largemouth bass, offspring may be exposed to increased predation when the parent is away during the angling event or when recovering from the angling stress (Kieffer et al., 1995; Philipp et al., 1997; Suski et al., 2003b; Steinhart et al., 2004). Effects on parental care behavior are further covered in the reproduction section below. If general fish health is reduced as a long-term effect of C&R angling, fish may also become more susceptible to predation, but no long-term studies of increased predation risk exist.

Predation of individual fish is difficult to record in nature, which explains the striking lack of studies of predation risk after C&R angling. In areas with high predator densities, predation may be an important mortality factor after release. This mortality may be reduced by refining handling and release procedures, and increased knowledge of factors affecting the predation risk is therefore needed.

Sublethal Endpoints

3. Injury. Tissue damage arising from the fish capture event is inevitable (Cooke and Sneddon, in press), especially in the vicinity of the hook penetration site. In general, the majority of fish are hooked in the jaw region (Muoneke and Childress, 1994). This area is important for respiration (ventilation), food acquisition and consumption, and in some

cases for reproduction (e.g., mouth brooding, competition for mates) or social interactions (e.g., yawning, displays; Cooke and Sneddon, in press). There are no scientific reports of the long-term consequences of jaw injuries. Meka (2004) noted that 29% of rainbow trout captured in a study in Alaska exhibited signs of previous capture, and more than 60% of the fish captured in this study received one or more significant injuries from that angling event. Another study on stream salmonids (rainbow trout, brown trout [*Salmo trutta*], and brook trout) in Wisconsin found previous jaw injuries on 6% of the captured fish (DuBois and Dubielzig, 2004). Another common location for sublethal injuries is the eye, resulting from damage during hooking and handling (e.g., Cooke et al., 2003a; DuBois and Kuklinski, 2004). In fact, DuBois and Dubielzig (2004) reported that 10% of stream salmonids landed experienced severe eye damage that was likely to cause long-term or permanently impaired vision. Lost or impaired vision in one eye does not imply that death is imminent, although it has been linked to mortality (Warner, 1976; Pauley and Thomas, 1993). However, individuals may suffer a fitness impact associated with finding prey, avoiding predators, or securing a mate. At present, there are no long-term assessments of visual impairments on the growth or fitness of fish.

The amount of bleeding following a C&R angling event is strongly dependent on the degree to which specific tissue is perfused and whether the injury includes specific damage to the cardiorespiratory system, such as the gills, heart, or vasculature. Injuries that result in substantial blood loss can result in immediate mortality prior to release (e.g., Pelzman, 1978). However, there are many instances where injuries include minor or moderate bleeding that is unlikely to result in mortality. It is difficult to provide specific descriptions to differentiate between bleeding that will be sublethal versus lethal. Pulsatile blood flow from a wound, indicating a direct and pressure-based connection to the vascular system, is perhaps the clearest indicator that the injury is major and potentially lethal. The level of bleeding described in most studies, where it is described as minor, simply refers to a slight pooling of blood in the actual hook wound. For fish living in marine environments, small amounts of bleeding may be relevant in the presence of sharks (Cooke and Philipp, 2004). Otherwise, unless there is major wound and significant blood loss, the bleeding will usually stop quickly, the wound will heal, and the fish will survive.

There can also be sublethal chronic injuries arising from lost fishing hooks or lures that stay in or on the fish. For example, when targeting powerful and toothy marine pelagic fishes, it is common to lose fish. Borucinska et al. (2001) found that a retained fish hook in a single blue shark (*Prionace glauca*) led to peritonitis and pericarditis. This was the first documentation of a pathogenic effect of a retained fish hook. In a more exhaustive survey, Borucinska et al. (2002) found retained fishing hooks from previous capture events in six of 211 (2.8%) blue sharks off Long Island, New York. The hooks were embedded within the esophagus or perforated the gastric wall and lacerated the liver. Collectively, tissue damage led to lesions including esophagitis, gastritis, hepatitis, and proliferative peritonitis.

Sublethal injury can also occur in the throat, esophagus, or gut from removal of hooks or leaving them in place. Some fish, such as white-spotted char, *Salvelinus leucomaenis*, are capable of expelling hooks that are left in place in due course (Tsuboi et al., 2006). A recent study revealed that recapture rates were similar between fish where hooks were left in versus those removed for 27 species in Australia (Wilde and Sawynok, in press). Diggles and Ernst (1997) reported that several fish were able to expel hooks during a post-capture holding period. Aalbers et al. (2004) reported that survival was enhanced in white seabass (*Atractoscion nobilis*) when deep hooks were left in, but growth rate was negatively affected. Similar results were reported by Schisler and Bergersen (1996) for rainbow trout. Schill

(1996) reported that 60% of deeply hooked wild rainbow trout were able to expel hooks. Thus, when hooks are left in fish, many times the injuries are sublethal.

4. Stress. Numerous studies have demonstrated that a C&R angling event is physiologically similar to burst swimming and results in a suite of hormonal, energetic, and ionic changes realized throughout a fish (Wood, 1991; Gustaveson et al., 1991; Kieffer, 2000; Suski et al., 2004). Specifically, burst swimming results in the anaerobic consumption of three endogenous fuels: phosphocreatine (PCr) and adenosine triphosphate (ATP), with glycogen being consumed when stores of PCr and ATP have been exhausted (Dobson and Hochachka, 1987; Hochachka, 1991), as noted in smallmouth bass collected by angling (Kieffer et al., 1995). Due to the anaerobic nature of these reactions, lactic acid accumulates as fuel sources are consumed (Hochachka, 1991; Pagnotta and Milligan, 1991; Wood, 1991; Wang et al., 1994). The dissociation of lactic acid into a lactate anion and a proton (H^+), combined with proton production from ATP breakdown (Hochachka, 1991), causes a pH decrease within the white muscle, and protons may leak out of the muscle resulting in an acidification of plasma as well (Wood, 1991; Wang et al., 1994), as was noted for striped bass (Thompson et al., 2002). This acidification can affect cellular structure or enzyme functioning (Lehninger, 1982), and the presence of protons within white muscle can also result in the osmotic shift of water out of the plasma and into muscle, thereby disrupting ionic/osmotic balance (Wood, 1991; Wang et al., 1994). This ionic/osmotic balance can also be disrupted as protons are actively excreted from plasma, and bicarbonate ion (HCO_3^-) is exchanged for chloride ions (Cl^-) at the gills in an effort to buffer acid/base disturbances (Wood, 1991; Wang et al., 1994).

Coupled with exhaustive exercise of C&R angling is the production of "stress hormones." Adrenaline and noradrenaline are two of the most common catacholamines in fish and are typically released immediately after the onset of exercise, while cortisol is the principal corticosteriod, with concentrations typically not peaking until 1–2 h following exercise (Barton et al., 2002). Secretions of stress hormones result in a suite of physiological and biochemical alterations to the internal physiology of fish to maintain performance during exercise, but shift the investment of energy from anabolic processes (i.e., growth and reproduction) to catabolic activities (i.e., energy mobilization and restoration of homeostasis) (Wendelaar Bonga, 1997).

For example, exercise raises the oxygen consumption of tissues, and stress hormones work to increase cardiac output, thereby raising blood circulation and oxygen delivery to tissues (Satchell, 1991). Such changes in cardiac output (and its components, stroke volume, and heart rate) have been noted following C&R angling for smallmouth bass (Schreer et al., 2001; Cooke et al., 2002b), rock bass (*Ambloplites rupestris*) (Cooke et al., 2001), largemouth bass (Cooke et al., 2002b, 2003b, 2004), and walleye (Killen et al., 2006). Stress hormones also cause the release of additional red blood cells from the spleen and an uptake of Na^+ and Cl^- by red blood cells, both designed to increase the amount of oxygen delivered to tissues (Pickering and Pottinger, 1995). Additionally, the production of stress hormones results in an increase in blood pressure, a dilation of gill vasculature, as well as increased gill permeability, all of which serve to increase the surface area available for gas exchange and improve oxygen uptake (Pickering and Pottinger, 1995; Satchell, 1991; Wendelaar Bonga, 1997). Catecholamine secretions also stimulate the conversion of glycogen stores to glucose to cope with increased energy demand in aerobic tissues such as gill and brain, thereby resulting in elevated levels of plasma glucose concentrations following the onset of many stressors (Gamperl et al., 1994; Wendelaar Bonga, 1997).

Despite the list of physiological changes that accompany a bout of angling (exhaustive exercise), most fish appear to be able to recover fairly easily. In general, the majority of

the physiological changes induced by a C&R angling event have returned to resting control levels within 2–24 h (depending on the variable being examined), provided the fish remains free from subsequent disturbances and in an oxygenated environment (Wang et al., 1994; Milligan, 1996; Richards et al., 2002; Suski et al., 2006).

5. Behavior. Behavioral measures of stress have proved to be sensitive indicators of the complex biochemical and physiological changes that occurs in response to stress (Schreck et al., 1997). Changes in behavior may be adaptive and increase the probability of survival or may reflect deleterious changes in how an animal senses and responds to its environment. Significant departures from behavioral norms may indicate altered success of food acquisition, predator avoidance, orientation, migration, and reproduction, and may therefore be suggestive of a decreased probability of survival (Schreck et al., 1997).

Several studies have recorded increased movement activity during the first hours and days after C&R angling (Sundström and Gruber, 2002; Gurshin and Szedlmayer, 2004; Thorstad et al., 2004) or, less frequently, decreased movement activity (Holland et al., 1993). C&R angling is also shown to alter upriver migration pattern in adult Atlantic salmon on their way to spawning grounds, with unusual delays, downstream movements, erratic movement patterns, and a reduced migration distance (Webb, 1998; Mäkinen et al., 2000; Tufts et al., 2000; Thorstad et al., 2003, in press). The reasons for altered movement and migration patterns after C&R angling are not known, but they could all be signs of deleterious stress effects. Furthermore, reduced activity may simply be a result of fatigue, whereas downstream movements may be an avoidance response to escape areas of "unfavourable conditions." The biological significance of such altered behaviors is not known, but it may be that in migrating species such as the Atlantic salmon, this may lead to a shift in the distribution of the spawning population within the river and disadvantages at the spawning grounds (Thorstad et al., 2003, in press). Few studies have looked into factors that influence behavioral responses, but Thorstad et al. (in press) found differences in behavioral reactions between Atlantic salmon caught and released during early and late stages of the upriver migration. Gurshin and Szedlmayer (2004) found no differences in movement patterns between Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) hooked internally or in the jaw.

Other changes in behavior, such as territorial, agonistic, schooling, and reproductive behaviors, may be induced by stress following C&R angling, but such aspects have rarely been addressed. Depressurization problems may also cause altered behavior, until the fish is able to regulate the air bladder pressure again with surfacing, and problems with getting down to deeper water (Bettoli and Osborne, 1998, see also the depth section below).

Competitive fishing may lead to relocation and concentration of fish, depending on the competition rules and release procedures. Release of a high number of fish in one or a few central sites has the potential to concentrate fish where they may be vulnerable to angling or deplete available food resources. Numerous studies of smallmouth and largemouth bass show varying results on whether displaced fish are returning to their site of capture or not and how far they disperse from the release site (e.g., Richardson-Heft et al., 2000; Bunt et al., 2002; Wilde and Paulson, 2003). Published and unpublished estimates were compiled by Wilde (2003), concluding that only 14% of tournament-caught largemouth bass and 32% of smallmouth bass returned to their site of capture. Smallmouth bass dispersed on average a greater distance (7.3 km) from their release sites than largemouth bass (3.5 km), and there was no difference in dispersal distances among fish captured and released in rivers, lakes, and reservoirs (Wilde, 2003). It has been recommended to transport fish for release by boat to distant and multiple release sites (Gilliand, 1999; Healey, 1990) and recommended against releasing fish at sites that have easy access and high angling pressure (Bunt et al.,

2002). Generally, the ability to return home after displacement seems to vary among species (Reingold et al., 1975; Lembo et al., 1999; Jepsen et al., 2001; Thorstad et al., 2001).

Are the same fish being captured over and over again in the C&R fishery? Recapture rates have especially been a subject for studies of smallmouth bass and largemouth bass fisheries (Burkett et al., 1986; Quinn, 1989; Hayes et al., 1997; Bunt et al., 2002), with little agreement whether released fish are subject to high or low rates of recapture (Wilde, 2003). A summary of studies concluded that 22% of largemouth bass and 15% of smallmouth bass released in fishing tournaments were subsequently recaptured by anglers (Wilde, 2003). Fish being recaptured up to 16–20 times have been reported (Burkett et al., 1986). Both smallmouth bass and largemouth bass seem to vary in their vulnerability to recapture, and individual vulnerability may vary among years (Burkett et al., 1986; Clapp and Clark, 1989). It has been suggested that recapture vulnerability is a heritable trait in largemouth bass (Burkett et al., 1986).

In common carp it has been shown that vulnerability to hooking decreased after one experience with a fish hook, but that the decreased vulnerability disappeared when the population was not angled for about one year (Beukema, 1970; Raat, 1985). Carp that were more vulnerable to angling showed better growth than carp that avoided the hook after a hook experience under an experimental condition of high stocking density (Raat, 1985). Also, in white-spotted char, individual fish varied in their vulnerability to recapture, and the probability of being recaptured increased with increasing body length, but was not related to growth or condition (Tsuboi and Morita, 2004). Males were more often recaptured than females (Tsuboi and Morita, 2004). Cutthroat trout (*Oncorhynchus clarkii*) in Yellowstone National Park were captured, on average, 9.7 times per season (Schill et al., 1986).

Atlantic salmon are rarely recaptured more than once during their river upstream migration (Webb, 1998; Whoriskey et al., 2000; Thorstad et al., 2003). Webb (1998) noted that exploitation rates in the Aberdeenshire Dee were similar to recapture rates of previously captured Atlantic salmon, implying no avoidance for being recaptured. In contrast, recapture rates of caught-and-released Atlantic salmon in the River Alta were only 4%, compared to exploitation rates of 50–70%, implying either avoidance for recapture or being more prone to capture during the early upstream migration phase compared to later in the season (Thorstad et al., 2003). Catch rates decreased rapidly after the introduction of angling in a previously unexploited rainbow trout population, which could partly be explained by possible behavioral shifts in fish after C&R (van Poorten and Post, 2005). Information on recapture rates in C&R fisheries is important both for the management of the fisheries, but also for the interpretation of catch statistics in studies of fish populations.

6. Fitness/reproduction. The fitness consequences of stress and, in particular, angling related stressors, have received very little attention from researchers. Disparate results obtained from the few existing studies create a continued need for studies that investigate fitness impacts (e.g., Booth et al., 1995). However, several studies have documented clear fitness impacts associated with C&R angling activities (Pankhurst and Dedual, 1993). There are many different ways in which C&R angling could alter fitness (see Table 1 in Cooke et al., 2002a). Because the reproductive period is essential for generating offspring to contribute to the populations, it is only logical to do everything possible to minimize sublethal stress during the reproductive period and allow the maximum contribution of offspring to subsequent year classes.

The largemouth bass is perhaps the best studied species with respect to the sublethal effects of C&R angling on fitness. That species provides sole male parental care. Evidence suggests that when nesting males are angled from their nest, even for a short period, the unprotected offspring are quickly consumed by predators, directly decreasing fitness (Philipp

et al., 1997). Even if fish are released after angling, Cooke et al. (2001) determined that when nesting males return to the nest, their locomotory activity is impaired for over 24 hours, and Suski et al. (2003b) showed that angling reduced the level of care provided to offspring by the attending male. A study by Ostrand et al. (2004) determined that large-mouth bass exposed to a simulated fishing tournament immediately prior to the spawning period produced fewer and smaller offspring than control fish.

In the aquaculture literature, extensive data suggest that salmonids exposed to acute and chronic stressors exhibit endocrine alterations that depress fitness (Campbell et al., 1992). Similar hormonal changes have been shown to occur in largemouth bass and walleye following bouts of angling (Suski et al., 2004; Killen et al., 2006), but the extent to which those hormonal changes can affect fitness have yet to be explored outside of an aquaculture setting. Effects on gamete viability or early fry survival as a consequence of C&R were not found in rainbow trout or Atlantic salmon (Pettit, 1977; Davidson et al., 1994; Booth et al., 1995). Two studies found that C&R of steelhead did not affect their return to spawning streams (Pettit, 1977; Hootin, 1987), and Lindsay et al. (2004) found that C&R did not influence the migratory behavior of Chinook salmon (*Oncorhynchus tshawytscha*). In one of the few marine examples, Lowerre-Barbieri et al. (2003) determined that common snook (*Centropomus undecimalis*) subjected to C&R angling did not immediately leave a spawning aggregation. However, some individual movement into and out of the aggregation site was observed during the spawning season, but spawning activity was not observed.

Fitness studies are difficult to undertake in field settings (Cooke et al., 2002a). For this reason, it will probably be many decades before there is a large body of work on the topic. Based on the negative consequences associated with angling during the reproductive period, as outlined above, it is only prudent for C&R fisheries to avoid capturing fish during the reproductive period (Cooke and Suski, 2005), unless data are generated that suggest that negative consequences are not observed for the species of interest.

7. Growth/energetics. Growth is an important and reliable indicator of fish health and population production. Fish growth is indeterminate and flexible, and fishes frequently respond to environmental changes and other factors with changes in their growth rate (Alm, 1959; McKenzie et al., 1983; Wooton, 1990). C&R may influence individual growth rates through, for example, physiological stress, physical injuries, increased susceptibility to diseases and parasites, behavioral changes, altered social rank, or other factors influencing feeding or energy consumption. Growth rates may, therefore, be a relevant indicator for whole-animal and long-term responses to C&R angling and a predictor of reproduction and population outcomes. Despite the advantages of using growth as an indicator of effects of C&R angling, few studies have covered this topic. The reason may be that studying growth effects based on mark-recapture methods in the field often imply difficulties with interpreting results, and long-term laboratory or semi-natural facilities for such studies are not easily available.

Negative effects of C&R angling on growth or condition factor have been demonstrated in striped bass (Diodati and Richards, 1996; also modelled by Stockwell et al., 2002) and rainbow trout (Jenkins, 2003; also modelled by Meka, 2003), whereas no effects were found in bream (*Abramis brama*) (Raat et al., 1997), white-spotted char (Tsuboi et al., 2002), pike-perch (*Sander lucioperca*) (Arlinghaus and Hallermann, 2007), or largemouth bass (Pope and Wilde, 2004). Surprisingly, growth rates were higher in hook-caught groups than in control groups of white seabass, which was explained by hook-caught groups being collected prior to control fish and, therefore, possibly incorporating a larger proportion of fish exhibiting aggressive feeding behavior (Aalbers et al., 2004). Hence, the latter study demonstrates some of the methodological challenges when studying growth effects. When

studying the effects of tournaments on fish, Siepker (2004) found that simulated tournaments reduced food intake. Bioenergetic simulations suggested that this would result in long-term growth reductions.

The effect on growth was dependent on bait techniques and hook type in rainbow trout and white seabass (*Atractoscion nobilis*) (Jenkins, 2003; Aalbers et al., 2004). Hook location had no effect in rainbow trout (Schill, 1996), but deeply hooked white seabass showed reduced growth compared to fish hooked in the mouth (Albers et al., 2004). Furthermore, growth appeared to be inversely related to the number of times hooked in smallmouth bass (Clapp and Clark, 1989).

Depressurization often harms fish hooked and retrieved from deep water, and swim bladder deflation may increase survival in released fish. Artificial swim bladder deflation did not impair growth in largemouth bass (Shasteen and Sheehan, 1997). After angling, fish may be temporarily stored in keep nets. No effect on growth by being held in keep nets was found for five cyprinid species after angling (Raat et al., 1997).

Growth is widely used as an indicator of effects of catch, handling, and tagging procedures in aquaculture (e.g., McCormick et al., 1998; Sørum and Damsgård, 2004) and tagging studies (e.g., Martin et al., 1995; Jepsen and Aarestrup, 1999). It is likely that we will see an increase in studies of growth effects also related to C&R angling in the coming years.

Systems Level Endpoints

8. Population/ecosystems. In many cases, the primary purpose of C&R is to enhance fish populations, as discussed elsewhere in this article. However, recent work has suggested that angling can directly impact fish populations, with effects possibly extending to aquatic ecosystems. Studies by Post et al. (2002), Almodóvar and Nicola (2004), and Sullivan (2003) all implicated angler activities in community-level changes such as population declines, reduced biomass, and altered age structure of fish (reviewed by Lewin et al., 2006). Those changes, however, are likely attributed to excess angler harvest coupled with particular ecological environments and life-histories (e.g., slow growth, old age at maturation). A single C&R angling event for an individual fish is not likely to have a discernable impact at the population or ecosystem level. However, if substantial portions of a population are repeatedly subjected to multiple C&R events (i.e., small population size or disproportionately large angling effort), if that high angling pressure is applied for a prolonged period (i.e., several reproductive cycles), or if C&R angling results in high cumulative mortality rates, then impacts at the population or ecosystem level may become visible. Few studies have directly related population or ecosystem level changes to C&R angling, likely due to challenges associated with a study such as establishing control groups, repeating experiments, and unequivocally assigning impacts to angling (Attrill, 2002). But monitoring of fish populations can be a useful way to ascertain the presence of population level stressors. Should the negative impacts of C&R angling be present at the population or ecosystem level, they would likely result from either chronic exposure to sublethal stressors or excessive individual mortality.

Following a C&R angling event, fish devote energy to recovering from stressors and restoring homeostasis rather than investing in growth, reproduction, or food acquisition (Wendelaar Bonga, 1997). As a result, the repeated capture and release of fish has the potential to reduce growth rate and result in a concomitant reduction in fecundity as energy is directed away from somatic and/or gametic endpoints toward physiological recovery. Several studies have indeed documented a link between an increase in stress hormone production and a decline in gamete quality (Pankhurst and Van Der Kraak, 1997), while

Ostrand et al. (2004) showed that stressors associated with competitive angling events can reduce offspring quality and fitness in largemouth bass. Production of stress hormones can also impair immune function, so fish that have been repeatedly caught and released may show an increased susceptibility to pathogens (Rice and Arkoosh, 2002).

As described in sections above, many aspects of a C&R angling event have the potential to act either alone or in concert to cause individual mortality (e.g., hooking location, temperature, depth of capture, etc.). Should a population of fish experience excessive, prolonged mortality from C&R angling, consequences may become visible at the population or ecosystem level that would be identical to those seen from excess harvest; high mortality rates due to C&R angling could result in changes in either the relative abundance of species within the community (composition) or in community properties such as absolute abundance, stock biomass, or food web dynamics (Shuter and Koonce, 1977; Micheli et al., 1999; Rochet and Trenkel, 2003). Organisms within aquatic ecosystems are interconnected with each other through direct and indirect interactions such as predation, competition, and mutualism (Reynolds et al., 2002). The removal of individuals through mortality can result in altered trophic cascades and changes to the ecosystem at many different levels, including alterations to primary productivity (Kaiser and Jennings, 2002; Lewin et al., 2006). The magnitude of population or ecosystem level changes resulting from C&R mortality, however, will depend on many factors, including the reproductive potential of the species/community, the rate of angler exploitation, the species composition of the community, and the carrying capacity of the community (Shuter, 1990).

To date, few studies have demonstrated a link between size-selective mortality through C&R angling and population or ecosystem level changes, but results from literature with marine fisheries suggest there may be potential for such changes to occur. Studies of marine and some freshwater fisheries have demonstrated that the regular, prolonged removal of the largest individuals in a population can impact the life-history characteristics of the entire population and result in a decrease in the age and size at maturation (Haugen and Vøllestad, 2001; Grift et al., 2003) and a dominance of the ecosystem by smaller individuals (Kaiser and Jennings, 2002). Additionally, Conover and Munch (2002) used laboratory simulations with Atlantic silverside (*Menidia menidia*) to show that the selective removal of the largest members of a population resulted in reductions of the mean weight of harvested fish and total harvest after only four generations. In freshwater populations, a shift to earlier maturation resulting from the harvest of large individuals is commonly called stunting and has been documented in several different fish species including bluegill (*Lepomis macrochirus* [Jennings et al., 1997]), brown trout (Anderson and Nehring, 1984), and rainbow trout (Anderson and Nehring, 1984).

Explanatory Factors for Various Endpoints

When a fish is hooked by an angler, there are many factors that can affect the outcome of the event for the caught-and-released fish. Ideally, the fish will survive the event, recover quickly, and experience no long-term sublethal impairments. At worst, the fish will die. Although anglers strive for the former outcome, it is often more probable that the outcome will be intermediate to these two extremes. Some of the factors that may affect the outcome are intrinsic, such as fish gender, age, previous exposure to stressors, maturity, condition, size, and degree of satiation. These intrinsic factors are largely outside the realm of factors that an angler can control or alter to benefit the fish, and, indeed, few of these factors have been studied with sufficient rigor to provide any conclusive statements for any species of fish. However, the environment in which the fish is angled and released can clearly

affect the outcome. Pertinent environmental conditions include abiotic factors, such as water temperature, hypoxia, depth or habitat complexity, as well as biotic factors, such as predator burden. Although these factors cannot be controlled by anglers, most of them can be readily assessed, and if deemed to be detrimental, the angler could release captured fish at an alternative location. The remainder of the factors that typically influence the outcome of an angling event can be controlled by the angler, including choice of fishing gear (terminal tackle and gear, such as bait/lure/fly type, hook type, rod, reel, and line) and angling practices (e.g., during the fight, when the fish is landed, and how it is handled and released).

The factors identified here most likely manifest themselves as a series of cumulative stressors, rarely acting independently (Wood et al., 1983; Cooke et al., 2002a). Angling mortality in salmonids has been suggested to be a two-stage process which emphasizes the inter-connectedness and cumulative nature of fishing impacts. Gjernes et al. (1993) suggested that injury location was affected by hook type and barb type in the first stage, and mortality was affected by injury location and species in the second stage. Here we examine the explanatory variables that mediate the presence and extent of the impacts on the endpoints listed above.

1. Bait and lure type. The choice of bait may impact mortality and injury for a C&R angling event. Artificial lures or flies tend to superficially hook fish, allowing expedited hook removal with minimal opportunity for damage to vital organs or tissue (Muoneke and Childress, 1994). Since the review by Muoneke and Childress (1994), there have been several comparisons of bait types. For example, Diggles and Ernst (1997) evaluated the effects of different lure and bait types on the hooking mortality of yellow stripey (*Lutjanus carponotatus*) and wire-netting cod (*Epinephelus quoyanus*). Baitfishing with single hooks caused significantly higher post-release mortality rates (5.1%) than did lure fishing with treble or single hooks (0.4%) and was the hooking method most likely to cause bleeding and damage to vital organs. Similarly, Pauley and Thomas (1993) revealed that cutthroat trout mortality rates were generally higher for fish captured on worm-baited hooks (40–58%) relative to those captured on lures (11–24%). Conversely, studies of both ling cod (*Ophiodon elongates*) (Albin and Karpov, 1998) and weakfish (*Cynoscion regalis*) (Malchoff and Heins, 1997) did not find any differences in mortality between fish captured on natural baits and those caught on artificial lures.

Studies of flies versus lures and bait have been consistent in that flies tend to be less injurious and have a lower chance of causing mortality. For example, Schisler and Bergersen (1996) contrasted the hooking mortality of fish captured on flies and lures and determined that mortalities were lowest by several fold for fly-caught fish. Meka (2004) also determined that rainbow trout captured on spinning gear (organic baits) tended to be injured more frequently than fish captured by fly fishing.

Even rigging type and fishing techniques with different bait can influence mortality and injury. For example, Schisler and Bergersen (1996) observed greater mortality among rainbow trout captured on artificial bait (slip-rigged artificial eggs) that were actively fished than among fish captured with the same bait fished passively. Similarly, Schill (1996) found that the frequency of deep hooking was greater among rainbow trout captured on a "slack line" than a "tight line." Orientation of bait on hooks affected survival of drift-caught Chinook salmon (Grover et al., 2002), in which greater mortality was observed when the bait was hooked head down as opposed to head up. Similar examples have been reported by Persons and Hirsch (1994) and Dedual (1996) for rainbow trout captured with different techniques.

2. Hook characteristics and types. Hooking of fish is an inevitable component of a C&R angling event, and various factors associated with hooking have the potential to impact the survival and well-being of released fish. Studies have shown that hooking consequences for angled fish can range from no appreciable impact (i.e., superficial hooking in jaw or lip) to blindness/eye injury, tissue damage, bleeding, esophogeal hooking, organ damage, or gill damage (Aalbers et al., 2004; DuBois and Kuklinski, 2004). Currently, it is believed that hooking location is the primary factor influencing the mortality of angled fish, with an increased probability of mortality following hooking in visceral areas such as esophagus or gills (Pelzman, 1978; Aalbers et al., 2004). There are a number of different hook characteristics and types, and these factors can impact the endpoints of a C&R event.

Hook type. The type of hook can greatly influence the anatomical hooking location (Lukacovic and Uphoff, 2002). For example, circle hooks (where the point of the hook is perpendicular to the shank rather than parallel to the shank) have been proven to have conservation benefits for a number of marine and freshwater recreational fisheries relative to conventional J-style hooks (Cooke and Suski, 2004). Circle hooks tend to result in shallower hooking relative to other hook types, thus reducing the risk of injuring important organs (e.g., heart, liver). In fact, circle hooks rarely hook in locations other than the corner of the jaw, although there are exceptions (see Cooke and Suski, 2004, for review). Subtle differences in the size of the hook can influence the ability of the hook to perform properly and lead to eye injuries (Cooke et al., 2003a). In addition, circle hook configuration (i.e., inline versus offline; Prince et al., 2002) can also dramatically alter the conservation benefits of circle hooks, with severely offset circle hooks tending to result in injuries and hooking locations similar to J-style hooks (Cooke and Suski, 2005).

A new hook design that shows promise for reducing or eliminating handling is the "self-releasing" Shelton hook (Jenkins, 2003; see their Figure 1). In a study of rainbow trout, mortality rates of fish caught on barbless circle hooks that had been removed were four times greater than those of fish captured on the barbless Shelton self-releasing hook (Jenkins, 2003). Shelton hooks can be removed without handling the fish when the angler pulls on a tag line that activates a release mechanism. The hook reverses direction by 180° and exits the fish when gentle pressure is applied to the main line. This type of novel gear design and creativity is needed by the recreational fishing industry to reduce injury and mortality of discarded fish.

Muoneke and Childress (1994) summarized early literature and reported that single hooks tend to be more deeply ingested relative to treble hooks. However, if treble hooks become deeply imbedded, they almost certainly will result in massive injury or mortality. Diodati and Richards (1996) also determined that treble hooks were associated with lower mortality rates than single hooks for striped bass because the latter were more likely to be swallowed, resulting in a greater occurrence of gut hooking. In their meta-analysis of salmonids, Taylor and White (1992) failed to demonstrate a difference in mortality between these two hook types. Jenkins (2003) reported that treble hooks and single baited hooks lodged in the esophagus of rainbow trout at similar frequencies. Conversely, Ayvazian et al. (2002) investigated the effects of different hook designs on hooking injury and mortality of tailor (*Pomatomus saltatrix*) in Western Australia. The authors reported that treble hooks resulted in a significantly greater mortality rate than other hook types. Although yield per recruit curves calculated using the sublegal fishing mortality estimate for each hook type were similar, yield per recruit calculated using treble hook mortality was lowest. The authors concluded that their current management strategies, including discouraging the use of treble hooks, should be effective in ensuring the survival of a high proportion of discarded tailor.

Among conventional hook types, the relationship between hook size, fish size, and hook performance varies widely among studies (Muoneke and Childress, 1994), perhaps due to interspecific variation. This prompted Muoneke and Childress (1994) to conclude that further research into the relationships between different hook types, size of hooks, and sizes of fish was warranted. In another synthesis-type article, Taylor and White (1992) conducted a meta-analysis on factors associated with hooking mortality in non-anadromous salmonids and concluded that hook size did not influence mortality rate. Similarly, Savitz et al. (1995) found no effect of hook size on mortality of coho (*Oncorhynchus kisutch*) or Chinook salmon in the Laurentian Great Lakes. However, Carbines (1999) studied the relationship between hooking mortality and hook size in blue cod (*Parapercis colias*) and observed no mortality among fish captured with 6/0 hooks, but noted significant mortality (25%) among those captured with smaller 1/0 hooks. In a recent study, Cooke et al. (2005) reported that hook size may be more important for anglers fishing with circle hooks than with other hook types. Apparently, circle hooks function most effectively when the entire hook can fit in the mouth of the fish and when the shank-to-point distance (gape) is large enough to permit jaw hooking (Beckwith and Rand, 2005; Cooke et al., 2005).

Barbed versus barbless hooks. Another factor that can influence the impact of a hooking event appears to be the presence or absence of a barb on the hook. Studies in this area have generally concluded that barbless hooks are less injurious and have reduced mortality rates relative to barbed hooks for a number of fish taxa (Muoneke and Childress, 1994), although disparate studies do exist (e.g., brook trout [DuBois and Kuklinski, 2004]). Use of barbless hooks has been shown to reduce the amount of time that is required by the angler to remove the hook by increasing the ease of removal (Diggles and Ernst, 1997; Cooke et al., 2001; Schaeffer and Hoffman, 2002; Meka, 2004) and reducing tissue damage at the point of hook entry (e.g., Cooke et al., 2001; Meka, 2004). Differences also may exist depending upon the type of hook (single or treble) and the type of bait (lure versus fly versus organic; see other sections).

Schill and Scarpella (1997) synthesized the results of past studies that directly compared hooking mortality of resident (nonanadromous) salmonids caught and released with barbed or barbless hooks. The authors determined that barbed hooks produced lower hooking mortality in two of four comparisons with flies and in three of five comparisons with lures; however, only one of 11 comparisons resulted in statistically significant differences in hooking mortality. The authors concluded that the use of barbed or barbless flies or lures plays no role in subsequent mortality of trout caught and released by anglers. Others have also suggested that barbless hooks provide little benefit, generating substantial controversy (e.g., Taylor and White, 1992; Schill and Scarpella, 1997; Turek and Brett, 1997). Nonetheless, the majority of data available support the notion that use of barbless hooks is beneficial for discards and can only benefit fish. Sublethal injuries and physiological disturbance (due to longer handling times) are more extensive with barbed hooks (Cooke et al., 2001), and for those reasons, barbless hooks can be an effective conservation and management tool.

Tackle configuration and hook type. Limited studies are available examining the influence of tackle configuration in association with hook types on injury of fish. However, there is strong anecdotal evidence from specialized carp angling that using fixed and heavy leads together with a short leader and a so-called hair rig can result in minimal deep hooking. In bottom fishing with heavy leads and short leader, the hair rig is an extension of the leader that fixes the bait outside the hook. The now free hook pierces the feeding carp as the carp moves away after sucking in the bait. When the fish swims against the heavy weight, the hook penetrates the lip instead of being deeply swallowed. The study of Beckwith and Rand (2005) on red drum (*Sciaenops ocellatus*) provided evidence that a similar mechanism can

occur with natural bait on the hook instead of using a hair rig. By using heavy leads and a short leader, deep hooking is minimized.

3. Angling duration. The duration that a fish is angled depends on the size of the fish (e.g., Thorstad et al., 2003; Meka and McCormick, 2005) and the equipment (i.e., how appropriately gear is matched to species/fish size in question) being employed. A number of studies have demonstrated that the magnitude of physiological disturbances experienced by an angled fish increase in magnitude with angling duration (Gustaveson et al., 1991; Kieffer et al., 1995; Thompson et al., 2002; Thorstad et al., 2003). Changes in plasma pH, increases in plasma cortisol, and increases of lactate in both plasma and white muscle all correlate positively with angling duration (Gustaveson et al., 1991; Kieffer et al., 1995; Tomasso et al., 1996; Gallman et al., 1999; Thompson et al., 2002; Meka and McCormick, 2005). This likely results from the prolonged burst exercise that accompanies angling, as well as the continued presence of stress hormones. In addition, larger physiological disturbances require additional time to correct and therefore may impact the ability of fishes to respond to future challenges such as predator avoidance. In fact, the length of time required for smallmouth bass cardiovascular variables to return to resting levels increased for exhaustively angled fish relative to briefly angled fish (Schreer et al., 2001). Nonetheless, longer periods of elevated cardiovascular variables indicated heightened metabolic rates as fish replenished their oxygen debt (Scarabello et al., 1991).

Coupled with the metabolic disturbances that accompany longer angling durations (lactate production, acid/base imbalance, energy store consumption, etc.), prolonged angling also results in significant ionic/osmotic disturbances (Gonzalez and McDonald, 1992; Tomasso et al., 1996; Gallman et al., 1999; Thompson et al., 2002). An unavoidable consequence of reduced gill permeability and increased gill surface area generated by stress hormones is a loss of ions (such as Na^+ and Cl^-) and uptake of water from the gills of freshwater fishes (Gonzalez and McDonald, 1992; Avella et al., 1991) or an influx of ions (such as Na^+ and K^+) and loss of water for marine fishes (Avella et al., 1991). Again, these disturbances may increase the likelihood of mortality for angled fish or may impair performance until disturbances have been corrected (Gonzalez and McDonald, 1992).

4. Competitive angling events. Competitive angling events (also known as angling tournaments) are competitions where contestants compete for the greatest catch of fish (weight, cumulative number, or total length), often of a pre-defined number of fish and typically within a pre-defined period of time (i.e., one day; see Schramm et al., 1991 for details). Most tournaments held today practice a live-release format where angled fish are returned alive to the water at the end of the day. In marine environments, where fish may be too large to easily transport to allow a direct comparison of different anglers' catches, comparisons are made on board using digital photography, impartial scrutineers, or the honor system where individuals verbally compare catches at the conclusion of the angling day. Fish angled in such tournaments in marine environments typically do not experience stressors beyond that of a non-tournament C&R angling event described above. However, a recent account from Australia reveals that some C&R angling events for estuarine fishes do include temporary retention in tanks (Broadhurst et al., 2005).

In North America, angling tournaments have grown in popularity to become a lucrative industry, with over 20,000 events held annually (Kerr and Kamke, 2003). Black bass (*Micropterus* spp.) are the most popular targets for these events (Kerr and Kamke, 2003), and anglers competing in black bass tournaments typically strive to obtain the greatest weight of five fish accumulated during an angling day. To accomplish this, fish are held on board vessels in livewells, and lighter fish are released when a heavier individual is caught (a

process known as culling). Livewells contain a pump to input fresh water to the tank and an overflow hole at the top, thereby allowing a continuous flow of water. Up to five fish can be held at any one time. At the conclusion of the angling day, all competitors report to a common site on the waterbody where their five fish are weighed in a porous basket on a scale. Following weighing, fish are released either at the point of weighing or distributed throughout the waterbody with a specially designed release vessel. Angling competitions are also popular among anglers in Africa, such as for large cichlids and tigerfish (*Hydrocynus vittatus*) in the River Zambezi. During a fishing competition in the Namibian sector of this river, 35% of the angled fish were released (Næsje et al., 2001), and the use of livewells in boats is common. The fate of released fish is particularly important in these areas where local people are dependent on the fish stocks as a protein source (Næsje et al., 2001).

Recent studies have shown that the physiological response of both largemouth bass and walleye sampled at the conclusion of angling tournaments is identical to that of fish following burst exercise depletion of anaerobic energy stores, secretions of cortisol, and an accumulation of lactate (Killen et al., 2003; Suski et al., 2003a). These physiological disturbances occur as a result of two distinct tournament sections: the angling event and air exposure associated with weigh-in (Killen et al. 2003; Suski et al., 2004), with full physiological recovery occurring <24 h following weighing (Suski et al., 2004). Additional stressors can be experienced by tournament-caught fish due to water quality and/or crowding in livewells (Kwak and Henry, 1995; Cooke et al., 2002b; Furimsky et al., 2003), elevated water temperatures (Wilde, 1998), wind speed/wave action (Goeman, 1991; Cooke et al., 2002b), and crowding in live-release vessels (Suski et al., 2005). Despite this complicated series of events, however, mortality rates following black bass tournaments have declined significantly over the past few decades, with most fish today released alive (Wilde, 1998).

5. Retention. C&R angling sometimes involves the retention of fish over a period of time (usually hours) prior to release. Professional anglers often hold fish in aerated livewells, whereas recreational anglers commonly use more affordable, readily available, and convenient methods, including stringers, fish baskets, and keep nets. Research has investigated the effects of keep net retention on the growth, survival (Raat et al., 1997), and stress response and recovery (Pottinger, 1997, 1998) of various cyprinid species. Additional research has focused on changes in water quality in keep nets during retention (Pottinger, 1997). Collectively, these studies suggest that retention is stressful to fish, but if provided with adequate water quality, mortality and sublethal disturbances are minimized. Cooke and Hogle (2000) compared six retention methods on smallmouth bass for 3- to 5-h periods: metal stringer through lip, metal stringer through gill arch, cord through lip, cord through gill arch, wire fish basket, and nylon keepnet. Control fish exhibited very little mortality (3%) and had negligible physical injury across all sampling periods. Most fish retained (95%) experienced some form of injury or mortality. Survival and injury varied among retention gears. In general, injury and mortality increased with increasing water temperatures, particularly when water temperatures were high. Gill damage or fungal lesions associated with abrasion and the cumulative stress of angling and retention appeared to be the precursors to most deaths.

6. Environment temperature. Because most fish are poikilothermic, changes in water temperature have pronounced impacts on metabolism (Fry, 1971), cellular function (Prosser, 1991), protein structure (Somero and Hofmann, 1997), enzyme activity (Lehninger, 1982), and diffusion rates for fish. Furthermore, the quantity of dissolved oxygen in water decreases with increasing temperature, potentially subjecting fish to reduced oxygen situation at elevated temperatures. As a result, fish that are caught and released at elevated water temperatures exhibit increased physiological disturbances (Gustaveson et al., 1991, Thompson

et al., 2002) and higher mortality levels (Atlantic salmon, Wilkie et al., 1997; Dempson et al., 2002; Thorstad et al., 2003; black bass, Wilde, 1998; striped bass, Wilde et al., 2000) relative to fish angled in cooler waters. Underlying the mortality at high temperatures in Atlantic salmon are limitations in maximal cardiovascular performance as fish approach their maximal metabolic rate (Anderson et al., 1998) and extreme biochemical alterations (Wilkie et al., 1996). Wilkie et al. (1997) determined that whereas warmer water may facilitate post-exercise recovery of white muscle metabolic and acid-base status in Atlantic salmon, extremely high temperatures increased vulnerability to mortality. Greater oxygen debt may also be correlated with higher water temperatures (McKenzie et al., 1996). Similarly, Gustaveson et al. (1991) noted that blood lactate accumulations in largemouth bass angled at 28–30°C were almost three-fold greater than fish angled at 11–13°C. The exact mechanism responsible for this relationship is not known, but may be due to a lack of environmental oxygen, a breakdown of cellular processes and protein structure/function at high temperatures (i.e. 'pejus' temperatures [Prosser, 1991; Somero and Hoffmann, 1997; Pörtner, 2002]), a reduction in cardiac scope that limits oxygen delivery to tissues (Farrell, 2002), or a reduction aerobic scope (Pörtner, 2002). In smallmouth bass, Schreer et al. (2001) found intermediate temperatures to be the best for recovery. Recovery from angling may be impaired in warmer waters relative to cooler waters, possibly due to the loss of cellular and sub-cellular performance at elevated temperatures (Suski et al., 2006), or due to reductions in dissolved oxygen availability. C&R angling at extremely cold water temperatures has also been suggested as potentially challenging to fish. However, Persons and Hirsch (1994) concluded that the lack of mortality for lip-hooked lake trout captured under ice suggested that capturing fish and handling fish in cold (i.e., subzero) temperatures had little effect on mortality. For northern pike angled through the ice, mortality was negligible for some groups, but increased for some hook types and deeply hooked fish (DuBois et al., 1994).

Individual species exhibit different thermal tolerances (Beitinger et al., 2000), and this must be considered for each species, population, and location. Most studies on the effects of water temperatures on fish tolerance in C&R angling have been performed in temperate areas of the world and very few under tropical conditions and high water temperatures. In tropical marine fisheries, most studies have been conducted at moderate temperatures, and thermal relationships are not as obvious (e.g., no effect of minor changes in water temperature on hooking mortality of common snook, Taylor et al., 2001). However, a study of freshwater cichlids in Africa showed that nembwe (*Serranochromis robustus*) and threespot tilapia (*Oreochromis andersonii*) suffered no direct mortality from C&R angling, even though water temperatures were 27–30°C during capture (Thorstad et al., 2004). For warmwater adapted species, low water temperatures may in fact be the conditions during which fish are more susceptible for stressful events such as C&R or other handling events. More than 300 Mozambique tilapia (*Oreochromis mossambicus*) and sharptooth catfish (*Clarias gariepinus*) died within two weeks in a laboratory tagging study in Namibia at 15–18°C (100% mortality), most likely due to too low water temperatures during handling and tagging of the fish, whereas most fish survived when the experiment was repeated at 22–25°C (Næsje et al., unpublished data). In that area, it is known by local fish farmers that Mozambique tilapia do not tolerate handling at such low water temperatures (15–18°C). Hence, what should be regarded as "high" and "low" water temperatures highly depend on the thermal tolerance of the species or stock and their acclimatization (Procarione and King, 1993; Zakhartsev et al., 2003).

If anglers continue to fish under extremely high and low water temperatures for the species and area in question, both the duration of the fight and handling time should be minimized. Ideally, fishing should be restricted during extreme water temperatures when

fish are theoretically most sensitive to stress (Cooke and Suski, 2005). In northern clines, there is need for additional research on the consequences of angling on fish at low water temperatures (i.e., ice fishing). Because water temperature exerts important control over almost all physiological processes in fish (Fry, 1971), extreme water temperatures are undoubtedly one of the periods when fish are particularly susceptible to mortality.

Oxygen. Temperature also influences oxygen availability, with high water temperatures resulting in marked reductions in dissolved oxygen. At present, we are unaware of any studies that evaluate the role of low dissolved oxygen in the natural environment on angled fish. However, there are several studies that have revealed the importance of providing fish with adequate water quality during livewell retention to minimize the lethal effects of hypoxia (e.g., Hartley and Moring, 1993; Furimsky et al., 2003; Suski et al., 2006).

Water hardness. Although it has received little attention to date, water hardness (the concentration of dissolved ions such as Ca^{2+}, Mg^{2+}, Na^{+}, Cl^{-}) has been shown to impact the stress response and survival of angled fish. Kieffer et al. (2002) showed that Atlantic salmon exercised in soft water (lower quantity of ions) exhibited a larger acid-base disturbance and increased mortality relative to fish exercised in hard water. Similarly, Diodati and Richards (1996) reported improved survival following angling for striped bass caught in saltwater (31‰) relative to fish angled in freshwater. Gallman et al. (1999) evaluated responses to exercise across salinity values of 17–33‰ but did not include salinity as a factor in their analyses. Thus, survival following release may be improved in harder water (or salt water) due to the availability of ions and an improved ability of fish to correct osmotic/ionic disturbances associated with angling.

7. Depth. The movement of organisms from deeper to shallower water is accompanied by a reduction in ambient pressure. During a C&R angling event, if a fish is hooked in deep water and quickly brought to the surface, the accompanying decline in ambient pressure can have profound physiological and physical consequences, especially in physoclistous fishes, where the swim bladder does not directly connect to the digestive tract. In particular, a rapid decline in ambient pressure has been shown to result in swim bladder inflation, often to the point of bursting or distension from the mouth (Feathers and Knable, 1983); rupturing of small blood vessels within the peritoneum, kidneys, and dorsal aorta (Feathers and Knable, 1983); external hemorrhaging (Feathers and Knable, 1983); formation of gas bubbles within the circulatory system, heart, gills and brain (Philp, 1974; Casillas et al., 1975; Feathers and Knable, 1983); and increased tissue damage (Morrissey et al., 2005) for a variety of freshwater and marine fishes.

Inflation of the swim bladder can also cause damage to internal organs through direct pressure and increase the probability of mortality. Gas bubble formation within the circulatory system can lead to increased blood coagulation that can cause blood clots (Casillas et al., 1975) and can also block blood flow to the heart and thereby increase the likelihood of cardiac failure (Beyer et al., 1976). The additional buoyancy that results from increased swim bladder volume forces fish to remain at the surface, where they may be subjected to heat stress, increased predation, or additional physiological disturbances as they struggle and try to return to depth (Keniry et al., 1996; St. John, 2003; Morrissey et al., 2005). External symptoms of decompression have been shown to arise in fish taken from as shallow as 3.5 m (Shasteen and Sheehan, 1997).

Studies involving largemouth bass (Feathers and Knable, 1983), red snapper (*Lutjanus campechaunus*; Gitschlag and Renaud, 1994), and dhufish (*Glaucosoma hebraicum*; St. John and Syers, 2005) have all concluded that the probability of fish mortality increases with depth of capture, possibly as a result of increased physiological trauma as fish ascend

from greater depths (Casillas et al., 1975; St. John and Syers, 2005; Morrissey et al., 2005). Feathers and Knable (1983), for example, documented that the mortality of largemouth bass depressurized from 9 m was approximately 25% but was almost 50% for fish depressurized from 27 m.

To combat the negative effects of depressurization and increase the survival rate of released fish, some researchers have suggested prohibiting C&R angling from great depths, while others have suggested venting, or 'fizzing.' Fizzing is a procedure during which the swim bladder of a decompressed fish is punctured with a hypodermic needle. Puncturing the swim bladder allows accumulated gas to escape and permits fish to return to a depth where recovery may be accelerated (Keniry et al., 1996; Shasteen and Sheehan, 1997; Collins et al., 1999).

To date, studies examining the survival of fizzed versus non-fizzed fish have generated disparate results. For example, Collins et al. (1999) noted that the survival of fizzed black sea bass (*Centropristis striata*) and vermilion snapper (*Rhomboplites aurorubens*) improved with fizzing, and Keniry et al. (1996) noted improved survival for yellow perch (*Perca flavescens*) with fizzing. Similarly, Shasteen and Sheehan (1997) and Lee (1992) reported increased survival in decompressed largemouth bass following swim bladder puncture. However, both Gitschlag and Renaud (1994) and St. John and Syers (2005) noted no increase in survival of fizzed red snapper (*Lutjanus campechanus*) and dhufish. Differences among studies may be related to species-specific physiology/anatomy, handling practices, or depth of capture. Keniry et al. (1996), for example, reported improved survival of fizzed yellow perch collected from 15 m depth, while Gitschlag and Renaud (1994) reported no benefit to fizzing of yellow perch collected from 50 m depth. However, Collins et al. (1999) reported >90% survival in reef fishes fizzed after collection from 43–55 m, further implicating species-specific anatomy/physiology in response to fizzing. Clearly, additional research in this area is needed before any recommendation on the efficacy of fizzing for additional fish species can be made.

Currently, the vast majority of state and provincial jurisdictions in North America do not promote fizzing for the angling public (Kerr, 2001), likely because of the potential for additional organ damage to fish should fizzing be done incorrectly. Rather, researchers have suggested preventing angling from excessive depths, giving fish a "decompression stop," whereby fish being angled are allowed to remain at an intermediate depth for a few minutes to permit the removal of accumulated gasses from their circulatory system (St. John, 2003), or using a submersible cage, harness, or hooks to improve the survival of decompressed fish upon release (Kerr, 2001).

8. Handling. Angled fish that are to be released typically need to be handled when they are unhooked. This period of handling can vary in many aspects and can have a considerable impact on the angled fish. When fish are exposed to air (such as that during unhooking or photography), their ability to uptake oxygen is severely impaired, and the amount of oxygen carried in blood drops substantially (Ferguson and Tufts, 1992). This results in increased anaerobic metabolism, the results of which are similar to that of burst exercise, consumption of anaerobic fuels, production of lactate, acid/base disturbances, etc., (Ferguson and Tufts, 1992). Additionally, the magnitude of physiological disturbance for air-exposed fish correlates positively with duration of air exposure (Killen et al., 2006), as does the time required for cardiovascular variables to return to control levels (Cooke et al., 2001, 2002b). A recent study revealed that brook trout swimming performance was drastically impaired at 120 seconds of air exposure (Schreer et al., 2005). Prolonged air exposure has been shown to increase mortality levels for fish during C&R angling events (Ferguson

and Tufts, 1992). Short-term mortality (12 h) was negligible for control rainbow trout and low for trout that were exercised to exhaustion but not exposed to air (12%; Ferguson and Tufts, 1992). When trout were exposed to air for either 30 or 60 seconds following exhaustive exercise, mortality increased to 38% and 72%, respectively. Based on those studies, it appears that air exposure, especially in fish that have experienced physiological disturbances associated with angling, can be extremely harmful, which is, however, not necessarily the case (Arlinghaus and Hallermann, 2007). Although different fish species will vary in their sensitivity to air exposure, anglers should attempt to eliminate air exposure when handling fish that are to be released in the water.

Landing nets are a simple and effective way for anglers to gain control of hooked fish and return them to the water, ideally with a minimum of stress or injury. Unfortunately, the use of nets can result in increased mortality and injury for angled fish. The epithelia covering fish skin produces a layer of mucus that contains both nonspecific and specific defense factors, such as immunoglobins, lysozymes, and proteases (Pickering and Pottinger, 1995; Wendelaar Bonga, 1997). When fish are handled during C&R angling (either by hands or by nets), there is an increased likelihood of removal of this protective mucus layer increasing the susceptibility to disease.

A study examining the impact of net materials on angled fish showed that different nets can inflict varying amounts of injury (fin abrasion), dermal disturbance, and mortality, likely due to the abrasive properties of the net (Barthel et al., 2003). Handling of fish also results in the production of stress hormones (Rice and Arkoosh, 2002) and cortisol secretions which cause suppression of the immune system, reduced immune cell function, and a concomitant increase in susceptibility to disease and pathogens (Anderson, 1990; Rice and Arkoosh, 2002). Currently, it is not known if pathogen infection following angling results from an increased susceptibility to environmental pathogens or to the increase of internal/opportunistic pathogens normally suppressed by a functioning immune system (Rice and Arkoosh, 2002). In addition, survivors of a pathogen outbreak often become carriers and can infect other members of the population through contaminated waste products (Anderson, 1990).

Angler ability also can affect how fish are handled and even how they are hooked. For example, Diodati and Richards (1996) and Meka (2004) reported that mortality among fish captured by more experienced anglers was lower than that observed among fish captured by less experienced anglers. In contrast, Dunmall et al. (2001) found no difference in mortality among experienced and inexperienced anglers but noted a greater incidence of deeply hooked smallmouth bass among those captured by experienced anglers. Newman and Storck (1986) emphasized the importance of handling techniques when dealing with specialized trophy fish like muskellunge (*Esox masquinongy*) and suggested that angler experience was likely an asset. Even in a river where experienced Atlantic salmon fly fishers were accompanied by professional guides, the handling time from landing of the fish to release was as long as an average of 3 minutes and 17% of the salmon were exposed to air (Thorstad et al., 2003). Such results indicate that there is a great potential for educating anglers in optimal handling of the fish.

9. Intrinsic factors. There are a number of intrinsic factors associated with individual fish that can also affect how they respond to C&R stressors. For example, within species, some researchers have revealed that fish respond differently to stressors at different life-history stages. Brobbel et al. (1996) compared the physiological response to angling in Atlantic salmon at two different stages of migration (kelts and bright salmon). This study demonstrated large differences in the degree of physiological disturbance that arose from

angling in the two migratory stages, with greater disturbance in bright salmon. In addition, angling-induced mortality was negligible for kelts but was 12% for bright salmon. Behavioral reactions after C&R may also differ between newly ascended Atlantic salmon and others that have stayed for a longer period in the river (Thorstad et al., in press). Furthermore, substantial intraspecific variation can exist among stocks/populations with respect to exercise physiology, environmental tolerances (Beitinger et al., 2000) and condition (Meka and McCormick, 2005), which could all result in variable responses to C&R angling. Mortality (Meals and Miranda, 1994) and physiological disturbance (Kieffer, 2000) can also vary with size of individual fish of the same species. For example, in a study of rainbow trout, Meka and McCormick (2005) reported that fish size can influence the duration of angling as well as the subsequent physiological stress because larger fish usually take longer to land than smaller fish. Hence, there usually is greater physiological stress for larger than smaller fish. In addition, sex may also play an important role in determining the consequences of catch-and-release angling; however, there are few tests of that supposition.

Quantitative Literature Review

Background. A quantitative literature review was conducted to understand trends in biological C&R research over time. We used the search engines Web of Science, Aquatic Science and Fisheries Abstracts, Fish and Fisheries Worldwide, and Google Scholar between August 14 and 16, 2005, to identify all studies on the biological consequences of C&R angling. A number of search strings (e.g., hooking mortality, stress, and angling) and search techniques (keywords, abstracts, full text, and cited reference searches) were used to maximize the number of records located. The majority of references located were from peer-reviewed accounts in periodicals and conference proceedings. We did not explore gray literature beyond that identified here but acknowledge that there are numerous theses and technical reports that do address biological issues associated with C&R angling.

For each paper located, a number of criteria were extracted. To broadly understand patterns of research, we classified all studies as either freshwater or marine. We also assessed the number of species studied in a single paper as 1, 2, or >2. The location of the studies was broken down by continent, but due to limited research in some regions, we collapsed studies into the following categories: North America, Europe, Australasia, and Other. To evaluate C&R research endpoints, we classified papers into the following categories: mortality, injury, stress, behavior, fitness/reproduction, growth/energetics, predation, and systems level. We also assessed the major explanatory variables (gear and practices) or study foci by categorizing studies as follows: competitive angling event, retention, handling, gear, bait, depth, and environment. For both evaluation of endpoints and explanatory variables, we selected all metrics that were applicable for a specific study (e.g., a single study could use mortality and injury as endpoints and use environmental conditions, gear, and bait as explanatory variables). All searching, summaries, and analyses were conducted by the same person.

Findings. We located 209 studies associated with the biological consequences of C&R angling using the aforementioned search engines (Table 3). The first study located by using the available search engines was published in 1957 (the first ever was probably Westerman, 1932), and it was followed by sporadic studies throughout the 1960s and 1970s (Table 3). Beginning in the 1980s, there was a substantial increase in published papers dealing with C&R angling, and progressive increases in research activity continue today (Table 3). In 1994, Muoneke and Childress effectively summarized the C&R studies on mortality to

Table 3
Temporal trends in the publication of studies on the biological consequences of catch-and-release (C&R) angling in freshwater and marine environments

		Frequency of C&R studies in different environments	
Study years	Metric	Freshwater	Marine
1975 and earlier	N	6	1
	% of total in environment	3.9%	1.8%
	% of total in period	86%	14%
1976 through 1985	N	17	2
	% of total in environment	11.1%	3.8%
	% of total in period	90%	10%
1986 through 1995	N	53	12
	% of total in environment	34.6%	21.4%
	% of total in period	82%	18%
1996 through 2005	N	77	41
	% of total in environment	50.3%	73.2%
	% of total in period	65%	35%
Total	N	153	56
	% of total	73%	27%

that point, and much of the current research activity has been influenced by their synthesis, conclusions, and suggested directions for future research. Not surprisingly, the Muoneke and Childress (1994) paper is currently the most cited C&R paper, with more than 60 citations as of 2005 (assessed using Google Scholar because Reviews in Fisheries Science was not tracked by the Institute for Scientific Information (ISI) in 1994, so it was not possible to use Web of Science Cited Reference Search. Google Scholar tends to yield more results than Web of Science because it also searches technical reports.).

Early C&R research was almost exclusively focused on freshwater fish (Table 3). In fact, the majority of the research was focused on two families, salmonids and centrarchids. Starting in the late 1970s, there were steady increases in the frequency of studies targeting marine species (Table 3). A recent synthesis by Cooke et al. (2002a) attempted to promote the use of novel technologies widely used in freshwater (e.g., telemetry) to understand C&R issues in marine environments. Those authors suggest that the vast nature of the ocean and logistic difficulties of working in marine systems (e.g., large fish, deep water) have retarded marine C&R research. Beyond that, there has also been the belief that the commercial fisheries sector is predominantly responsible for the global fisheries crisis. Only recently has the recreational fishery been considered (Cooke and Cowx, 2004) or implicated (Coleman et al., 2004) in global fishery declines. Perhaps a pivotal point in marine C&R research was the marine C&R symposium held in 1999 (work published in Lucy and Studholme, 2002). Indeed, since the late 1990s, there has been a large increase in C&R work in marine systems (Table 3). It is our judgment that only now is there an appropriate balance between C&R research in marine and freshwater environments. Nonetheless, based on the early emphasis on freshwater research, only approximately one-fourth of all studies are marine (Table 3).

Table 4
Temporal trends in the publication of studies on the biological consequences of catch-and-release angling conducted in different continents

		Continent			
Study years	Metric	North America[1]	Austral–Asia[2]	Europe[3]	Other[4]
1975 and earlier	N	7	0	0	0
	% of total in Period	100%	0%	0%	0%
1976 through 1985	N	19	0	0	0
	% of total in period	100%	0%	0%	0%
1986 through 1995	N	60	2	0	0
	% of total in period	97%	3%	0%	0%
1996 through 2005	N	91	15	11	4
	% of total in period	76%	12%	9%	3%
Total	N	177	17	11	4
	% of total	85%	8%	5%	2%

[1]Studies conducted in the USA and Canada.
[2]Studies conducted in Australia, Japan, and New Zealand.
[3]Studies conducted in countries of the European Union.
[4]Studies conducted in the Caribbean and Africa.

The regional focus of C&R studies was initially limited to North America, and this trend continued until the 1990s (Table 4). This is not surprising considering the popularity and economic importance of North American fisheries and the resultant high angling pressure. With increased interest in angling for recreation and the growing concern over the sustainability of global fisheries, there has been a recent increase in C&R research beyond North America (Table 4). Australasia has been the leader outside America, with 17 studies (Table 4). However, the research activity has only occurred in three countries, with most in Australia and fewer in New Zealand and Japan. Europe has also been the focus of some C&R research with most occurring in the Netherlands (e.g., Raat, 1985; Raat et al., 1997), with fewer examples in other countries such as Norway (e.g., Thorstad et al., 2003), the United Kingdom (Hickley, 1998; Pottinger, 1998; Webb, 1998) and Russia (Whoriskey et al., 2000). Some research is ongoing in Germany (Arlinghaus and Hallermann, 2007). In this jurisdiction, C&R research has to focus on undersized fish due to the current guidline not to release legally sized or otherwise unprotected fish (Arlinghaus, 2007). The only other locales where C&R research has occurred is in Africa (Thorstad et al., 2004) and several countries in the Caribbean and Central America (e.g., Cooke and Philipp, 2004).

The scope of C&R studies also has changed over time. For example, early research was almost always focused on a single species (Table 5). The majority of studies today are still focused on a single species; however, there are increasingly more studies that contrast two species or multiple species (Table 5). The two-species contrasts have typically been focused on related species such as smallmouth and largemouth bass (Furimsky et al., 2003), bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) (Cooke et al., 2003a), and various stream salmonids (DuBois and Dubielzig, 2004; DuBois and Kuklinski, 2004). The multi-species (>2 species) studies tend to focus on complex marine fisheries where it is not possible to selectively target an individual species (e.g., reef fisheries; see Schaeffer

Table 5
Temporal trends in the publication of studies on the biological consequences of catch-and-release angling relative to the number of species considered in an individual study

		Number of species covered		
Study years	Frequency metric	1	2	>2
1975 and earlier	N	4	2	1
	% of total in period	57%	29%	14%
1976 through 1985	N	17	1	0
	% of total in period	94%	6%	0%
1986 through 1995	N	42	17	5
	% of total in period	66%	27%	7%
1996 through 2005	N	93	12	15
	% of total in period	78%	10%	12%
Total	N	156	32	21
	% of total	75%	15%	10%

and Hoffman, 2002; Broadhurst et al., 2005). Although we did not quantify them, there were several studies that looked at intraspecific variation? usually comparing different populations (Cooke et al., 2004), waterbodies (Suski et al., 2003a), hybrids (Newman and Storck, 1986), or origin (e.g., wild versus hatchery; Wydoski et al., 1976). Overall, these studies were quite rare.

The majority of early C&R studies were conducted in the field. There are a growing number of studies that have been conducted in laboratories (e.g., Ferguson and Tufts, 1992; Schreer et al., 2001; Furimsky et al., 2003), experimental ponds/enclosures (Cooke et al., 2000; Aalbers et al., 2004), or combinations of laboratories/field settings (Cooke et al., 2001; Suski et al., 2004). There also are a growing number of C&R studies relying on biotelemetry (reviewed in Cooke et al., 2002a) to remotely monitor physiological responses, including stress and recovery, of free swimming fish to C&R (Anderson et al., 1998; Cooke et al., 2003b), as well as their post-release behavior (Mäkinen et al., 2000; Cooke et al., 2000; Whoriskey et al., 2000; Cooke and Philipp, 2004) and their ultimate fate (Jolley and Irby, 1979; Dormier et al., 2003; Thorstad et al., 2003; Cooke and Philipp, 2004). There are also a number of research contributions that provide detailed information on how to use telemetry and other tagging methods to quantify release mortality (Pine et al., 2003). Although not quantified, we also noted increased use of "controls" in mortality studies where fish are captured using non-angling techniques (e.g., electrofisher, seine, traps [Warner, 1976, 1979; Warner and Johnson, 1978; Dempson et al., 2002]), which is the only possible way to assess the consequences of the confinement where mortality is monitored.

The most common type of C&R research conducted to date involves assessment of hooking mortality (Table 6). Early C&R research always used mortality as an endpoint (100% of studies prior to 1975), whereas more recently there has been additional focus on sublethal consequences, with approximately 70% of studies using mortality as an endpoint after 1995 (Table 6). The most common sublethal factor that was examined was physical injury (Table 6), which tells little about the long-term consequences of an angling event. This metric follows similar trends to hooking mortality in that it was almost universal in early studies, but has been replaced by alternative sublethal indicators in recent studies (Table 6). Nearly one-fourth of the studies we located considered some physiological indicator of

Table 6

Temporal trends in the publication of studies on the biological consequences of catch-and-release (C&R) angling with different endpoints. Studies with multiple endpoints were recorded in all appropriate columns. Thus, although data were extracted from 209 studies, there were 333 total endpoint measurements

		C&R Endpoint							
Study years	Metric	Mortality	Injury	Stress[1]	Behavior[2]	Fitness[3]	Growth[4]	Predation	Systems level[5]
1975 and earlier	N	7	2	0	0	0	0	0	0
	% of total in period	78%	22%	0%	0%	0%	0%	0%	0%
1976 through 1985	N	14	6	6	1	2	0	1	0
	% of total in period	48%	20%	20%	3%	6%	0%	3%	0%
1986 through 1995	N	60	24	9	0	3	1	0	2
	% of total in period	61%	24%	9%	0%	3%	1%	0%	2%
1996 through 2005	N	73	44	34	19	10	6	3	6
	% of total in period	38%	23%	17%	10%	5%	3%	1%	3%
Total	N % of total	154	76	49	20	15	7	4	8
	% of total	46%	23%	15%	6%	5%	2%	1%	2%

[1]Includes physiological studies.
[2]Includes migration, movement, and activity studies.
[3]Includes all assessments of fecundity, gamete quality, reproductive hormones, parental care activity, and reproductive behavior.
[4]Includes bioenergetic studies.
[5]Includes population and community assessments.

stress when assessing C&R (Table 6), such as white-muscle disturbance (e.g., Kieffer et al., 1995), plasma hydromineral status and stress hormones (Suski et al., 2004), and cardiac activity (Anderson et al., 1998; Cooke et al., 2003b). Interestingly, most studies assess mortality or stress but rarely both (see Ferguson and Tufts, 1992; Wilkie et al., 1997). Between 1996 and 2005 there were 118 C&R studies, of which 73 focused on mortality and 34 included physiological stress indicators (Table 6). Other sublethal metrics, such as behavior, reproduction/fitness, and growth/energetics are clearly important, but have only been considered since the 1990s (Table 6). Common behavioral metrics include swimming activity (Dormier et al., 2003) and migration (Thorstad et al., 2003; Mäkinen et al., 2000), while common reproductive/fitness indicators include assessments of parental care activity (Philipp et al., 1997), spawning behavior (Lowerre-Barbieri et al., 2003), gamete quality and quantity (Booth et al., 1995), and reproductive success (Ostrand et al., 2004). Although more limited, there are several recent examples of bioenergetic analyses (Stockwell et al., 2002) and growth assessments (Pope and Wilde, 2004) (Table 6). There is also a growing interest in studies that document post-release predation (Jolly and Irby, 1979; Cooke and Philipp, 2004; Thorstad et al., 2004) (Table 6). Higher-order research such as systems level (e.g., populations, communities) is still underrepresented (Table 6), although there have been some studies in recent years (e.g., Anderson and Nehring, 1984; Perry et al., 1995; Schneider and Lockwood, 2002; Thorstad et al., 2003).

A number of causal factors (i.e., explanatory variables or topics of interest) have been considered when evaluating C&R angling effects, largely summarized by Muoneke and Childress (1994), Cooke and Suski (2005), and Bartholomew and Bohnsack (2005). For example, one suite of factors considered important deals with the environmental conditions during/after angling (Table 7). Although we did not quantitatively summarize which environmental factors were chosen, research was overwhelmingly focused on evaluating or considering water temperature and its interaction with C&R. Most of these were focused on warm conditions (e.g., Wilkie et al., 1996, 1997; Wilde et al., 2000; Dempson et al., 2002), but several also evaluated low temperature or ice fishing conditions (e.g., DuBois et al., 1994; Dextrase and Ball, 1991). Oxygen limitations or hypoxia were the second most common (e.g., Hartley and Moring, 1993; Furimsky et al., 2003), with most of those related to confinement of black bass in livewells. Overall, approximately 25% of all C&R studies considered an environmental factor as an explanatory variable (Table 7). Water depth also has been recognized as an important explanatory variable but only recently and only in five studies (Table 7).

Another suite of factors is associated with the practices of the anglers and their gear (Table 7). For example, reflecting general concern for competitive angling events (see Schramm et al. 1991), approximately 13% (32 of 309) of all C&R studies to date have focused on assessing their specific consequences. This work has almost exclusively covered freshwater species, emphasizing the black bass and walleye events in North America and the coarse fisheries (e.g., bream) of Europe (Raat et al., 1997). These studies have evaluated the effects of different retention gears (e.g., livewells, keepnet, stringers; Raat et al., 1997; Cooke and Hogle, 2000) as well as their operation (Kwak and Henry, 1995). Handling in general has also been recognized as an important explanatory variable in recent years (e.g., approximately 15% of studies between 1995 and 2005; Table 7) and, in particular, air exposure duration (Ferguson and Tufts, 1992; Cooke et al., 2001). There have also been several studies on gear used to assist in landing or handling fish such as nets (Barthel et al., 2003). By far the most common explanatory variable is the gear type (see Muoneke and Childress, 1994, for detailed coverage). This can include hook type (single, double, or treble), hook design (circle or J; Cooke and Suski, 2004), hook size, and presence/absence

Table 7

Temporal trends in the publication of studies on the biological consequences of catch-and-release angling with different primary explanatory variables. Studies with multiple endpoints were recorded in all appropriate columns

		Primary explanatory variables						
Study years	Metric	Environment[1]	Depth	Gear[2]	Bait[3]	Handling[4]	Competitive events[5]	Retention[6]
1975 and earlier	N	1	0	6	1	0	0	0
	% of total in period	13%	0%	74%	13%	0%	0%	0%
1976 through 1985	N	4	0	6	4	2	1	1
	% of total in period	22%	0%	33%	22%	11%	6%	6%
1986 through 1995	N	22	1	23	10	4	15	10
	% of total in period	26%	1%	27%	12%	5%	17%	12%
1996 through 2005	N	21	4	36	13	18	16	8
	% of total in period	18%	3%	31%	11%	16%	14%	7%
Total	N	48	5	71	28	24	32	19
	% of total	21%	2%	32%	12%	11%	14%	8%

[1]Includes primarily water temperature, hypoxia, and ice cover.
[2]Includes primarily hook type, hook size, and presence/absence of barb.
[3]Includes bait, lure, and fly type.
[4]Includes handling related activities such as air exposure and use of landing nets.
[5]Includes explicit studies of the effects of competitive angling events such as tournaments and derbies.
[6]Includes studies on the effects of different retention gear (e.g., stringers, keepnets, livewells).

of the barb. The other major explanatory variable associated with gear is the choice of bait. This can include lures, flies, live bait, organic bait, scented baits, etc. There are indeed a number of other explanatory variables that have been studied infrequently but are worthy of mention, including angler experience (Dunmall et al., 2001) and bait/lure size (Wilde et al., 2003b; Arlinghaus et al., unpublished data).

Summary of Biological Aspects of Catch-and-Release

Using information from our comprehensive synthesis, we developed a tabular summary for the likely magnitude of impact on C&R angling endpoints associated with the primary explanatory variables (Table 8). The purpose of this synthesis is to summarize what we know about the biological aspects of C&R and, more importantly, identify what key knowledge gaps need to be addressed. There are a number of key conclusions that we were able to draw from this tabular summary (Table 8) and our broader review on the biological aspects of C&R.

1. Most research effort to date on C&R has focused on mortality and injury as endpoints. These studies are useful for making inferences about general effects. However, mortality rates vary extensively among species and among studies for a given species (see Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005, for detailed summaries and tables, including most mortality studies available to date).
2. All aspects of C&R can contribute to stress and/or injury and have the potential to result in mortality. A fish cannot be handled without eliciting a stress response. Similarly, a fish cannot be angled without the hook causing physical injury. Our purpose in noting this here is that this also provides a way forward. If we accept that these effects occur, then we can focus efforts on trying to minimize those negative aspects of C&R angling. This perspective is not new and simply recognizes that fishing of any kind, including other sectors such as commercial and artisanal, has the potential to have negative effects on fish, fisheries, and the environment (Cooke and Cowx, 2006).
3. In general, we know very little about the population level impacts, growth/energetics and fitness/reproduction, and behavior. In fact, there is a need within the entire C&R community to attempt to generate links that cross biological levels (e.g., does a stress response in an individual fish cascade up to a population level impact?) to make findings more relevant to fisheries management activities. Indeed, there is a close link between the endpoints mortality and fitness/reproduction and, to some extent, also growth and population effects. Variables that likely or possibly lead to mortality most often also lead to at least possible reproduction and growth effects and thereby potentially to population effects. Variables likely or possibly causing mortality do not imply that all fish are being killed; some fish may suffer reduced condition but still survive. These fish possibly or likely also suffer from reduced reproductive success, reduced growth, etc.
4. There is an enormous amount of variation in many factors that affect the biological consequences of C&R angling. One question that has arisen is: Do we need species-specific guidelines for C&R? (see Cooke and Suski, 2005, for lengthy discussion). For example, there are differences in angling gear, fishing techniques, environments, ability, etc. There is also substantial variation in the biology and sensitivity of different species, populations, sex, and individuals. Even the same individual may have different sensitivity at different times of the year or different periods of their life-history (e.g., juvenile, adult, reproductive period, etc.). Thus, for now, the summary material presented here or elsewhere becomes a simplified generalization on which managers and anglers

Table 8

Likely magnitude of impact on catch-and-release (C&R) angling endpoints associated with the primary explanatory variables (categorized as Unlikely, Possible, or Likely) and the relative amount of information that we have on each topic (categorized as None, Some, or Well-studied). Here we have further divided some of the explanatory variables to make this summary table more useful. Categorizations reflect what we know about various mechanisms

Explanatory variables	Potential impact and our knowledge of a particular relationship	Potential C&R endpoints/effects							
		Mortality	Predation	Injury	Stress	Behavior	Fitness/ Reproduction	Growth/ Energetics	Population/ Systems
Bait	Potential impact	Likely	Possible	Likely	Likely	Unlikely	Possible	Possible	Possible
	Knowledge	Well-studied	None	Well-studied	Some	None	None	None	None
Gear–Terminal Tackle	Potential Impact	Likely	Possible	Likely	Likely	Unlikely	Possible	Possible	Possible
	Knowledge	Well-studied	None	Well-studied	Some	None	None	Some	None
Gear–Light vs. Heavy	Potential Impact	Possible	Possible	Unlikely	Likely	Possible	Unlikely	Possible	Possible
	Knowledge	Some	Some	None	Some	Some	None	None	None
Landing Gear–Nets	Potential Impact	Possible	Possible	Likely	Likely	Unlikely	Possible	Unlikely	Possible
	Knowledge	Some	None	Some	None	None	None	None	None
Competitive Events	Potential Impact	Possible	Possible	Possible	Likely	Possible	Possible	Possible	Possible
	Knowledge	Well-studied	None	Some	Well-studied	Some	Some	Some	Some
Other Retention	Potential Impact	Possible	Possible	Likely	Likely	Possible	Possible	Possible	Possible
	Knowledge	Some	None	Some	Some	None	None	None	None
Handling	Potential Impact	Possible	Possible	Likely	Likely	Possible	Possible	Possible	Unlikely
	Knowledge	Some	Some	Some	Well-studied	Some	Some	Some	None
Environment (temp)	Potential Impact	Likely	Possible	Unlikely	Likely	Possible	Possible	Possible	Possible
	Knowledge	Likely	Possible	Unlikely	Likely	Possible	Possible	Possible	Possible
Depth	Potential Impact	Likely	Likely	Likely	Likely	Likely	Possible	Possible	Possible
	Knowledge	Some	None	Some	Some	Some	None	None	None
Intrinsic	Potential Impact	Possible	Possible	Unlikely	Likely	Likely	Possible	Possible	Possible
	Knowledge	Some	Some	None	Some	Some	Some	Some	None

can base their recommendations as regards C&R. Moreover, information summarized in this paper may be quite useful for species for which no data exist.

5. We have made great strides in understanding the biological consequences of C&R since the first study in 1957. As evidenced by the increasing absolute number of studies, as well as the fact that they are being conducted on more species and using multiple endpoints, C&R biological science is emerging as a unique field of research, with the most promising aspect of this beyond simply documenting problems or negative consequences. Almost every study has some specific management implication. And much research is now being devoted to developing or refining strategies for minimizing the negative consequences of angling or particular types of angling, such as tournament fishing. For example, some forms of fishing tournaments typically expose fish to a large suite of potentially stressful factors (e.g., air exposure, exercise, confinement, temperature, etc.), and research can show how to ameliorate potentially negative influences on the fish. Bringing research into practice will require partnering among academics, government researchers, fisheries managers, industry, angling organizations, and most importantly, anglers. Indeed, many of the changes we have seen in the recreational fishing sector with respect to how fish are handled during C&R really have emerged as a result of anglers, managers, and scientists working together.

Potentials and Pitfalls of Catch-and-Release

C&R, in its various forms, is but one of a set of management alternatives available to fishery managers and must be viewed in that context. Indeed, C&R regulations would be difficult to implement in the absence of any other regulations and, as mentioned throughout this paper, are often derived from them (e.g., as a result of minimum size limit regulations; Policansky, 2002). Important management tools that are associated with regulatory C&R include various regulations on harvest, such as seasonal closures, daily bag limits, size-based limits, and annual quotas (Arlinghaus et al., 2002). Most fishing regulations, even if they do not specifically mandate C&R, require it for compliance (Policansky, 2002). Any size or bag limit, for example, requires the live release of a fish caught that is outside the limit; in some places, capture of a bag limit requires that fishing cease in that water (e.g., Chinook salmon in some Alaska rivers). Similarly, seasonal and species closures require the same. In addition, voluntary C&R is popular among certain angler groups (Fayram, 2003). However, common to all regulations that demand C&R or voluntary C&R is their uncertainty concerning their effectiveness and the potential biological and social downsides associated with it (Wilde, 1997; Radomski et al., 2001; Sullivan, 2003). Thus, the devil lies in the details, as the obvious advantage of C&R to reduce fishing mortality while facilitating and promoting angling use can lead to various social and biological potentials and pitfalls. Some of them are briefly discussed below (see also Table 9 for summary).

Potentials

Social Benefits. Catch among anglers is often highly skewed to the left, which suggests that most anglers catch few or no fish, and most of the fish (>50%) are caught by a relatively small number of highly effective anglers (Baccante, 1995; Arlinghaus, 2004). Those more successful anglers often are also the most highly committed fishers that adhere to voluntary C&R. C&R by the most successful anglers can thus help to preserve fish in the population for the catch by other less successful anglers or for conservation of fish popultions for their own sake (Gresswell and Liss, 1995). Therefore, C&R can enhance the quality of the angling

Table 9
Potentials and pitfalls associated with catch-and-release fishing broken down into social and biological aspects (see text for details)

Category	Issues
Social benefits	• Preservation of angling opportunities and associated economic and social benefits (cf. Arlinghaus et al., 2002), including tournament angling
	• Meeting of catch-dependent angler satisfaction; quality fishing experience
	• Allows fishing on contaminated waters
	• Formation of aquatic stewardship, environmentally-responsible behavior
	• Facilitates development of fish-friendly gear
	• Preserves unique resources (e.g., trophy fish)
	• Helps in research and fisheries management
	• Joins diverse angler groups
	• May create respect for nature and wildlife
Biological benefits	• Conservation of fisheries resources
	• Conservation of keystone species and components of the ecosystems (e.g., large, fecund individuals)
	• Preserve ecosystem services generated by fish (Holmlund and Hammer, 1999)
	• Reduction of selection pressure by angling
Negative social impacts	• Loss of management tool (voluntary C&R)
	• Education needed for best practices
	• Monitoring of angler catches more problematic
	• Intrasectoral conflicts between anglers
	• Intersectoral conflicts within society
	• Catchability as new common-pool resource
	• Enhancement of catch expectation (unrealistic level)
Negative biological impacts	• Lethal impacts
	• Sublethal impacts
	• Potentially stunting

experience for many anglers and, hence, encourage satisfaction and participation and promote the continuous generation of a multitude of economic, social, and ecological benefits to society (Gresswell and Liss, 1995; Arlinghaus et al., 2002). This helps not only the industries that are dependent on angling participation or the agencies with budgets dependent on angling but also helps many anglers to derive a catch-dependent, satisfactory angling experience (Arlinghaus and Mehner, 2005; Arlinghaus, 2006). Social benefits of angling include quality of life and various cultural, social, psychological, and physiological benefits, while economic benefits encompass economic impacts within the economy and economic value to the individual angler over and above current expenses (consumper surplus) (Arlinghaus et al., 2002). C&R is at the cornerstone of tournament angling and angling (eco)tourism at high-profile and extremely valuable fisheries (Policansky, 2002; Zwirn et al., 2005). C&R is also the only possibility for allowing fishing in waters contaminated with PCBs or other

noxious substances (Orciari and Leonard, 1990). However, contaminated fish might be less resilient to C&R related stress.

Available information on the economic benefits of recreational fishing has been reviewed in Arlinghaus et al. (2002) and Cooke and Cowx (2006). It currently is impossible to reliably estimate the economic importance of recreational fishing on a global scale because information is incomplete, and different jurisdictions use different definitions and methodological approaches. However, even a partial estimate is impressive: adding together partial estimates for annual angling-related expenditures from Cooke and Cowx (2006) for the United States (freshwater) and 10 countries in western Europe, Australia, and Canada, with a partial estimate for U.S. marine recreational fisheries (NMFS, 2006), gives a total of more than $U.S. 76 billion spent per year on recreational fishing in recent years. It would be of great additional use to estimate the economic impact to regional and national economies and the net economic value accruing to individual anglers of C&R angling, because many management, political, and business decisions could be thereby informed. In addition, C&R is increasing as a proportion of recreational fishing, as described throughout this paper. Unfortunately, it currently is almost impossible to make such an informed estimate because C&R is part of all recreational fishing. Some empirical work nevertheless suggests that the economic importance of fisheries that largely depend on C&R can be substantial (Holland et al., 1998; Arlinghaus and Mehner, 2003; Chen et al., 2003; Ditton and Stoll, 2003; National Mullet Club of the United Kingdom, 2006). For example, the net economic value (consumer surplus) attached to one day of total C&R fishing in the Yellowstone National Park was estimated between $US 172 and $977, translating into a total economic value of up to $US 385 million per year for angling in the park (Kerkvliet et al., 2002). In a different study in Pennsylvania, per day expenditure and net economic value per trip were found to be higher for C&R trout fishing with tackle restrictions (fly fishing only) than for various other outdoor recreational opportunities, such as wildlife viewing and C&R fishing without tackle restrictions (Shafer et al., 1993). It is safe to conclude that C&R angling provides significant economic benefits to society and angling communities worldwide.

Social benefits of C&R extend these named economic and social dimensions, if C&R helps the angler to become more aware about ecological processes and if C&R helps to increase environmental concern and the appreciation of an increasingly urbanized society for life and nature (Evans, 2005). Moreover, fisheries research can benefit from C&R if angler-assisted tagging programs are implemented that provide insights into the biology and ecology of exploited fish species (Costello, 2000; Lucy and Davy, 2000). Angler-assisted tagging programs can also improve aquatic stewardship among individual anglers (Lucy and Davy, 2000).

Thus, C&R has the obvious benefit of allowing fishing to occur with reduced or no depletion of the fish populations being targeted. Hence, it allows conservation of ecosystem components while still allowing fishing (recreation) to occur. For example, within one ecosystem, anglers might be allowed to harvest an abundant population, while a threatened species is protected by C&R. C&R allows not only multiple captures of an individual fish, but allows remarkably large (and valuable) fish to be caught more than once, and in direct contrast to kill tournaments and other fishing involving retention of large fish it encourages new records and fascinating angling experiences by allowing the rare, exceptionally large fish to continue to grow.

Pleasure and conservation are the hallmarks of C&R, and, in the wake of the conservation angle, there is also considerable interest in C&R in relation to fishery management (Policansky, 2002). On which waters and in which form C&R makes sense in terms of conservation and fishery management is for the fisheries manager or the angler community or

society at large to decide locally, regionally, or nationally. More importantly, in the present context, is the observation that C&R unites the most diverse kinds of anglers in purpose. There could hardly be more contrasting social and environmental backgrounds than, for example, fly-only salmon fishing, big game fishing for billfish, bonefish stalking, the carp hunter, the bass fishing competition angler, and fishing the canal on Sunday just for the sake of it. Only C&R has caused anglers of all kinds to think in terms of angling rather than in terms of their individual recreational activity.

The successful practice of C&R also requires knowledge and good practice. In order to be successful, C&R anglers must be well-informed and good stewards for aquatic resources: the right handling of the fish depends on knowledge. That knowledge has, thanks to the practice, grown over time, and all anglers today benefit directly from that knowledge, which would not be available without C&R.

C&R has given angling new impulses. The debate it stimulates throws "conservative" anglers back on to their fundamental assumptions as the "guardians of the rivers" (Bate, 2001), a position that anglers have lost in some jurisdictions to other stakeholders such as nature conservation groups (Schwab, 2003). If an angler opposes C&R, he or she must also be prepared for the fact that dearly held prejudices and parochial lore will come under scrutiny. On a practical level, angling owes the growing popularity of barbless hooks to C&R. Without C&R, barbless hooks would not have made the progress they have, nor would there be any discussion of the relative merits of circle and J hooks. Finally, the practice of C&R forces anglers to reflect on their activities and allow tackle innovations to flourish which reduce adverse impact on fish welfare (Arlinghaus et al., 2007).

Biological Benefits. Recreational fishing is increasingly being recognized as measurably affecting fish populations, if fishing intensity and the associated intentional or unintentional mortality is large (NRC, 1999; Post et al., 2002; Sullivan, 2003; Almodóvar and Nicola, 2004; Cooke and Cowx, 2004, 2006; Lewin et al., 2006). In such situations, the value of C&R fishing, partial or total, regulatory or voluntary, lies in the conservation of fishery resources. Often, C&R angling programs are introduced as an alternative to ordinary catch-and-kill recreational fishing to protect declining populations, if the alternative reduce fishing effort is considered unacceptable. The available evidence suggests that such programs can be very effective (Gresswell and Liss, 1995). Whoriskey et al. (2000), for example, suggested that the implementation of C&R regulations for a population of Atlantic salmon in the Russian Federation helped increase the abundance of juveniles in the population. Carline et al. (1991) found that C&R contributed to a sustained high density of trout in Pennsylvania. Sullivan (2003) reported that an adaptive management plan that included imposed C&R regulations in Alberta, Canada, helped improve the catch rates of walleye that were previously overexploited. Thorstad et al. (2003) demonstrated that the numbers of Atlantic salmon spawning redds more than doubled after the imposition of mandatory release regulations for a river in Norway, and Schneider and Lockwood (2002) showed that C&R regulations on predatory fish could be implemented as part of a management program to improve stunting problems in bluegill populations in the United States. Modelling studies supported the empirical findings about the stock conserving effects of appropriate C&R regulations, provided that hooking mortality and sublethal effects are low or minimal (Clark, 1983; Waters and Huntsman, 1986; Allen et al., 2004).

The value of conserving large and old fish for successful recruitment and as a measure to reduce recruitment variability is beginning to be appreciated on a global scale (Conover and Munch, 2002; Birkeland and Dayton, 2005). Recreational fishing is typically

size and age selective, and exploited populations typically experience a profound age and size truncation over the minimum size limit (e.g., Pierce et al., 1995; Almodóvar and Nicola, 2004; reviewed by Lewin et al., 2006). Thus, under intensive angling use, partial C&R of a portion of the caught fish or the implementation of slot length limits (combinations of minimum and maximum size limits) can help to counter age and size truncations under selective angling mortality. The few studies that have looked at the effects of C&R to conserve large and old fish have shown positive effects. For example, catch rates of trout in C&R areas in Colorado were 48% greater than in control sections, and the abundance of large fish was 28 times greater (Anderson and Nehring, 1984).

C&R can also help to minimize the selection pressure that recreational fishing might exert. Fishing in general exerts selection pressure on fish populations and causes evolution in fish (Policansky, 1993a, 1993b; Lewin et al., 2006). Angling vulnerability has been shown to have a heritable component that correlates positively with fitness-related traits, such as aggression, metabolic rate, and parental care (Cooke, 2002). Moreover, there is some evidence that fish that are more vulnerable to the angling gear are also the dominant individuals (Lewynsky and Bjornn, 1987) or those that show higher growth potential (Favro et al., 1979). Releasing a portion of the more vulnerable fish can reduce the evolutionary potential of recreational fishing and help to maintain the ecological and genetic integrity of exploited fish species (Lewin et al., 2006). The same is true for immature fish, because C&R of these fish allows future reproduction provided that immature fish are released unharmed. In fact, this idea is at the heart of most minimum-size regulations across the world and accepted as a good idea by most anglers.

Pitfalls

Negative Social Impacts. Promoting C&R can also have various negative social consequences and create new challenges for fisheries management. For example, voluntary C&R can lead to a loss of management tools if it undermines the effectiveness of minimum-length limits or other traditional harvest limits (Quinn, 2001). Moreover, promoting C&R means increased education efforts for managers to inform anglers about best practices to increase survival of released fish. Also, standard creel surveys may provide wrong signals about the resource state if significant underreporting of released fish occurs (Quinn, 2001).

Social conflicts also occur in response to C&R (Arlinghaus, 2005). Either illegal harvest rates are significant in some fisheries, creating conflicts between anglers and fisheries managers (Sullivan, 2002), or among-angler conflicts take place because supporters of C&R and supports of consumptive angling disregard each other's interests (Arlinghaus, 2005). Moreover, there is abundant anecdotal and some scientific evidence that fish learn from the experiences of being caught and released and, as a result, become more difficult to catch (Beukema, 1970; Raat, 1985; Policansky, 2002; Youngs and Hayes, 2004). Therefore, catchability becomes a new common-pool resource, increasing the rivalry in consumption to catch a fish first, which happens in many specialized carp fisheries in Europe, in which selected trophy fish are only caught once or twice a year. Fish populations in C&R sections can also become so abundant that the popularity of those sections dramatically increases. This in turn can lead to crowding and can reduce the angling experience due to congestion rather than due to unsatisfactory catch quality; in such cases, space becomes the common-pool resource instead of the fish, and this change requires different approaches to management (Policansky, 2001).

Social conflicts also occur across different stakeholder groups, e.g., when anti-angling movements, whose ethical underpinnings are reviewed above, lobby against C&R (Arlinghaus, 2005). For example, People for the Ethical Treatement of Animals (PETA) and the Humane Society of the United States (HSUS) oppose C&R fishing, describing, along with some fish biologists (e.g., Balon, 2000), C&R as entertainment by torturing animals (Quinn, 2001). In Germany, the issue of C&R has created abundant social and legal conflicts, and anglers releasing trophy fish have been assessed monetary fines for cruelty to animals (Arlinghaus, 2007).

Some stakeholders say that C&R is a fig leaf for pleasure and profit maximization (e.g., tournament fishing). If, for example, one reads in an angling magazine that anglers can catch 50 Pacific salmon a day and release them all, one might be tempted to ask whether their pleasure would have been lessened had they caught only 40 fish, or stopped at 30 or 20 or 10 or 2. Do anglers who catch 50 salmon a day still see something around them? The obsession with quantity (fish, income) is not specific to C&R: it can be found throughout angling and throughout society (Schwab, 2004); excesses of individual anglers due to lack of knowledge or moral education are not specifically C&R-related (Schwab, 2004). However, if fish abundances are maintained by C&R in some places, the practice might contribute to unrealistic catch expectations among anglers elsewhere that challenge their support for other aspects of fisheries management (Arlinghaus and Mehner, 2005).

Negative Biological Impacts. The effects of C&R on fished populations have been reviewed in this paper and elsewhere. It can be concluded that as a management tool, C&R has usually achieved the aim of allowing for increased fishing pressure without depleting the fish populations. However, as discussed here, C&R can also lead, under certain situations, to substantial mortality and manifold sublethal impacts on the individual fish. Hence, biological impacts of importance can occur, which led Bartholomew and Bohnsack (2005) to question total C&R as a practice in no-take marine reserves (see Cooke et al., 2006, for a different perspective). Several studies have shown that C&R-associated mortality on some species can be larger than the harvest-associated mortality (Diodati and Richards, 1996; Sullivan, 2003; Radomski, 2003), and the cumulative impacts can be high (Walters and Martell, 2004). Other researchers have suggested that C&R might be so successful that it leads to undesirable stunting, because there is no predation on the population in danger of stunting (e.g., Gerard, 1998, for roach in Belgium), but such an effect cannot apply to a natural ecosystem, i.e., one with the full complement of natural predators.

Some angler practices can encourage the biological downsides of C&R and, thus, require special mention. The seeking of line-class records in particular, i.e., seeking records based on a minimum line strength, encourages angler behavior that affects fish adversely, because it often leads to longer times required to land the fish. However, the number of anglers actively seeking line-class records probably is small enough that there is no significant population effect on any species.

To sum up, C&R is not a free lunch, because it does affect fish populations through hooking mortality and sublethal impacts. The impacts of C&R need to be increasingly integrated into population models that mimic the impacts of traditional harvest regulations (Diodati and Richards, 1996; Post et al., 2003).

Research Needs

As evidenced by the depth and breadth of materials covered in this paper, there currently is a large and comprehensive literature that has examined many different aspects of C&R

angling. Despite this volume of work, however, there are still a number of future priorities that we conclude should be addressed to improve our understanding of C&R issues and to better manage recreational fisheries for the future. Key C&R research topics are summarized in Table 10, broken down into social and biological research needs. In particular, we draw attention to the actual and potential value of comprehensive angler surveys such as the Marine Recreational Fisheries Statistics Survey conducted by the U.S. National Marine Fisheries Service (NRC, 2006). Such surveys have the potential to provide much valuable information about angler attitudes, behavior, motivation, expenditures, C&R rates, etc., especially if problems of bias and comprehensiveness are solved, if methods are developed for adequately evaluating the extent and effects of C&R, and if more comprehensive human-dimensions information is included in the surveys (NRC, 2006). Such large-scale surveys are not restricted to the United States at present, but they are not sufficiently widespread (e.g., Roy Morgan Research, 2003, 2004; Arlinghaus, 2004; see other examples in Pitcher and Hollingworth, 2002a).

Recommendations for improving the understanding of the C&R behavior of anglers were provided by Ditton (2002) and NRC (2006). Recommendations for improving natural scientific approaches to understanding the biological impact of C&R were given by Cooke et al. (2002a) and Pollock and Pine (2007). Aas (2002) emphasized the need to understand fishing across cultural and national boundaries, including improving scholarly communication across those boundaries. Thus, there is enormous potential for improved collection of data and insights if angler surveys are used productively, collaboratively, and synthetically, and if scientific rigor is increased in socioeconomic studies on angler C&R behavior and biological studies on the impact of C&R on the ecology of exploited fish populations.

Conclusions and Implications for Management and Conservation

While releasing a portion of one's catch has always been at the heart of conservation across the world, many cultures resist its use as a management tool or an acceptable angler ethic. However, if recreational fishing is not wrong, then C&R cannot be wrong, because it is, in one form or another, an integral part of angling and common worldwide under certain regulations. In any case, recreational fishery managers in all countries are encouraged to investigate regional cultural issues surrounding C&R, if advocating its use. Managers need to have at their disposal the widest array of tools possible to maintain fisheries while providing angling opportunities, and C&R can constitute a valuable one, if properly applied. There are many conflicts surrounding C&R regulations that might be eased by changes in language or communicative quality and by particular consideration of the values of stakeholders affected by C&R fishing.

Issues based on cultural norms of attitudes toward fish, such as the central and eastern European and widespread aboriginal tradition of fish as food, or C&R angling being vilified as an elitist practice, have long and continuing histories in many parts of the world. These issues may have serious implications when managers opt for the use of C&R regulations. Time spent researching local cultural norms of behavior toward fish may prove of value when shaping the language of fisheries regulations. Managers may have control over some of the factors that influence angler decisions to keep or release caught fish (e.g., situational factors such as size or type of fish caught); however, other factors are beyond immediate management influence (e.g., centrality of fishing to an angler's lifestyle). Whereas education and outreach efforts may work to influence some anglers orientation toward conservation, releasing fish, and the use of proper techniques, the results of the human dimension studies

Table 10
Summary of key catch-and-release (C&R) angling research needs

Research category	Catch-and-Release research need	Rationale and key points
Social	Understand the attitudes, beliefs, norms, and motivations underlying C&R behavior	In particular, research is needed to understand the extent to which conservation concerns influence C&R behavior and how this influence varies according to species (or population, stock, etc.) targeted. Studies should initially focus on understanding the relationships among beliefs about possible conservation-oriented outcomes of practicing C&R, attitudes toward fisheries conservation, and C&R behavior. More work is also needed to understand how various fishing motives influence C&R behavior.
Social	Understand the processes whereby anglers come to adopt C&R behavior	Future studies should aim to understand the process whereby anglers come to adopt C&R behavior. An important question is: Do anglers who adopt C&R follow a developmental process whereby they become increasingly dedicated to the C&R philosophy? And, if so, does this process parallel a process of development in fishing in general (Bryan, 1977; Ditton et al., 1992)? An important aspect of this line of research will be understanding the socialization process through which anglers learn the attitudes, norms, and skills appropriate and necessary for participation in C&R fishing (Kelly, 1977), and understanding how this socialization process influences which anglers adopt the C&R behavior and why they do so. Understanding how and why C&R becomes the norm within certain segments of the angler population will be important for outreach and education efforts aimed at increasing the acceptance of the C&R philosophy within the angler population.

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Table 10
Summary of key catch-and-release (C&R) angling research needs *(Continued)*

Research category	Catch-and-Release research need	Rationale and key points
Social	Compare predictors of C&R across different angler sub-populations	Results of previous studies suggest that much of the future research on C&R behavior should be conducted and replicated primarily at the angler sub-population level (i.e., angler populations segmented by species targeted and/or location). Important questions include: Do the predictors of C&R behavior vary across angler sub-populations? Likewise, does an angler's C&R behavior vary according to the choices made about what species to target and where to fish (i.e., within which sub-population an individual's fishing activity takes place)? Do factors such as norms of conservation, norms of C&R behavior, and anglers' perceptions of fishery health vary across angler subpopulations and, if so, how does this influence C&R behavior? And finally, how and why has C&R become so firmly established in some fisheries compared to others? Research with angler populations outside North America, particularly from areas where the norms and attitudes surrounding C&R fishing differ from those in North America (e.g., Europe; Aas et al., 2002), will be critical for gaining better answers to these questions. Much of the human dimensions research on C&R of anglers to date has focused on the USA.
Social	Understand public attitudes and beliefs regarding C&R	Studies are needed to examine how society views C&R and particular forms of C&R in order to gather basic data that support current animal welfare-related conflicts in some jurisdictions. Moreover, studies need to be conduced that investigate how anglers view C&R and about their willingness to adopt practices that increase survival of the fish.

Table 10
Summary of key catch-and-release (C&R) angling research needs *(Continued)*

Research category	Catch-and-Release research need	Rationale and key points
Social	Understand the role of C&R in facilitation of aquatic stewardship and respect for nature	Evans (2005) proposed that C&R is a visible sign of an enrooted respect for nature, here the individual fish. Research, both theoretical and empirical, that examines this proposition is needed to understand the social implication of the (voluntary) C&R ethic of anglers. There has been some discussion in Maine (ASF, 2006), as elsewhere, about the advisability of allowing careful C&R even for endangered species to preserve an angling constituency for them. In other words, if nobody is allowed to fish for Atlantic salmon at all, then who will care enough to try to protect them and their habitats? We are not aware of documentation of the benefits and adverse effects of allowing such fishing; the discussion is an important one and is likely to develop further.
Social	Understand C&R as a source of conflicts between stakeholders	Conflicts surrounding C&R are increasing world-wide. Research is needed that examines which underlying reasons explain such conflicts. Until now, only qualitative models exists (e.g., Arlinghaus, 2007).
Social	Understand the economic benefits and consequences of C&R	Information is needed on how much anglers value C&R angling, how they respond to C&R angling opportunities, and how much of their time and money they spend on C&R, opposed to other forms of recreational fishing. This research can be accomplished by focused studies on limited areas or species that are characterized by C&R angling exclusively or almost exclusively. In addition, broader, comprehensive surveys are needed to develop information on trends and aggregate data on expenditures. Because the charter and guiding industries are of crucial importance to understanding angler behavior, they need to be included in the studies as well (Policansky, 2002).

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Table 10
Summary of key catch-and-release (C&R) angling research needs *(Continued)*

Research category	Catch-and-Release research need	Rationale and key points
Biological	Expand inter- and intra-specific assessments of catch-and-release	Existing studies have focused on several high profile species (Cooke and Suski, 2005). There is a need to expand to include research on alternative species. In addition, there can be substantial intra-specific variation (e.g., sex, life-stage, size, etc.) that needs to be considered in catch-and-release studies. These data could be used to develop conceptual models of the impacts of catch-and-release within and among species. For all the above social research questions, well-designed and comprehensive surveys have great potential for being useful; because of the scope of the research, such surveys typically will need to be conducted by or with the support of national governments or on a national scale.
Biological	Conduct controlled experiments to document the disturbance and recovery trends of blood and muscle biochemistry, hormones, and the cardio-respiratory system	Controlled laboratory assessments can be used to manipulate factors, such as the duration of air exposure, degree of exhaustion, and water temperature, to determine how these factors may contribute to sublethal disturbances or mortality and how they alter recovery duration.
Biological	Assess the sublethal effects of angling-related behavior on growth and other fitness-related variables	Growth and other fitness-related indices can be affected by catch-and-release angling either directly through reduced food intake or indirectly through sublethal acute or chronic stress (see Cooke et al., 2002a). Much opportunity exists for development of bioenergetics models to assess the costs associated with different angling practices. See Cooke et al. (2002a) for comprehensive list of possible fitness alterations, such as reductions in gamete quality and quantity.

Table 10
Summary of key catch-and-release (C&R) angling research needs *(Continued)*

Research category	Catch-and-Release research need	Rationale and key points
Biological	Evaluate animal welfare aspects of catch-and-release, including the development of techniques to minimize injury and stress	A large body of research on animal welfare has recently been developed for aquaculture (Huntingford et al., 2006), and there is a need for similar research activities in the recreational fishing industry. Essentially, the concepts associated with considering welfare of angled fish are identical to those associated with ensuring that fish are released in the best possible condition (see Cooke and Sneddon, in press).
Biological	Evaluate the link between physiological stress and longer-term behavior and survival	Catch-and-release angling results in a suite of predictable and easily quantifiable physiological disturbances for fish. By relating the magnitude and source of these disturbances with angling-induced mortalities, managers and scientists can begin to better understand the reasons for mortality in angled fish and ultimately use this understanding to modify and improve angling techniques to minimize mortality.
Biological	Evaluating the consequences of deep-water capture (decompression) on fish as well as techniques for mitigating these effects	Capture of fish from deep water can lead to catastrophic physiological changes and, in some cases, mortality, yet little is known about the longer-term consequences of this activity. In addition, the efficacy of manual air bladder deflation ('fizzing') at improving the survival of deeply-angled fish needs to be investigated, as studies on this topic to date have generated disparate results. Additional research can hopefully establish critical angling depths for different species, as well as effective mitigation techniques that can be employed to maximize the survival of released fish.

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Table 10
Summary of key catch-and-release (C&R) angling research needs *(Continued)*

Research category	Catch-and-Release research need	Rationale and key points
Biological	Evaluate the impacts of hook retention on fish health, survival, and behavior	Effort should be directed towards determining the impacts of leaving hooks in the tissue of released fish when the hook is set deep in the esophagus. Also, there is a need to monitor post-release behavior in fish where hooks or lures are left inside the fish, as happens when the line breaks. When fish are hooked deeply, anglers often expend a great deal of effort attempting to remove the hook, and such efforts can result in prolonged air exposure and/or significant tissue damage for fish that will ultimately be released. Currently, the tradeoffs between such air exposure and/or tissue damage compared to leaving deeply imbedded hooks in fish are not known. Understanding the nature of this trade-off can have implications for the way that deeply hooked fish are handled prior to release.
Biological	Evaluating the effects of catch-and-release angling across biological levels, particularly the population	Little is known about the effects of catch-and-release angling at the level of the population, community, or ecosystem. Such information is essential for development of management tools and strategies. There clearly is need for more research on these topics, which will require creativity and likely an interdisciplinary approach (e.g., bringing together behavior, physiology, and endocrinology in field and lab settings). Moreover, catch-and-release study results, e.g., mortality, need to be integrated into standard stock assessment models to foresee the population effects of catch-and-release in a "model experiment" (e.g., Millard et al., 2003).

Table 10
Summary of key catch-and-release (C&R) angling research needs *(Continued)*

Research category	Catch-and-Release research need	Rationale and key points
Biological	Evaluating the interactive effects of multiple stressors	To date, most stressors and injuries have been considered independently. For example, a study of air exposure typically would not assess the potential interactive effects of water temperature, fish size, or fish sex. Future research must reflect the growing recognition that stressors are additive and might be size, age, or temperature dependent.
Biological	Increasing the rigor of catch-and-release studies through better experimental design and use of controls	Much of the existing research on catch-and-release (particularly hooking mortality) fails to utilize controls. This requires capturing fish using non-angling techniques (e.g., electrofishing, seining, etc.). Another common problem is pseudoreplication, where different treatments are held in non-replicated tanks. There is also a need to move beyond conducting hooking mortality studies in cages/pens/tanks to include telemetric or tagging studies in the field.
Biological	Linking quantitative description of angling fisheries (e.g., catch rates, total number of fish hooked and handled per year, way of handling in realistic settings) and catch-and-release studies	In many cases, a wealth of information is available about the impact of catch-and-release on individual fish. However, there are limited studies that linked classical fisheries biological studies and description of angling fisheries with catch-and-release studies.

reviewed in this paper suggest that fisheries managers must have realistic expectations as to the role C&R will likely play in fisheries conservation. Although some anglers may become highly dedicated to the C&R philosophy, available evidence suggests that a substantial number of anglers will practice C&R only in some situations or not at all. Although C&R is, and will continue to be, an important fisheries management tool, managers should be careful to avoid alienating large segments of the angling public with C&R regulations and avoid the appearance of valuing one type of resource use (i.e., C&R) over others. To meet the needs of their diverse clientele, management agencies and C&R anglers will need to continue to recognize that keeping fish is a valid use of fisheries resources in many cases.

Conflicts among anglers, conservationists, and fisheries managers might occur because anglers might want to continue C&R fishing on species that are endangered or in no-take protected areas. We have reviewed in this paper abundant documentation that hooking mortality is not zero, even though it can be less than 1% in some cases. For example, fishing for officially listed endangered species under Section 9 of the U.S. Endangered Species Act is prohibited. The act prohibits the take of a listed endangered species. Take is broadly defined and includes any activity that increases the mortality rate of that species, even by a small amount; it also includes harassment. Thus, at least in some cases, it is not possible to fish legally for an endangered species. As an example, in Maine, all fishing, including C&R, for Atlantic salmon, which are federally listed as endangered in some, but not all, streams there, was prohibited from 2000 until September 2006, when a limited C&R fishery was allowed in the Penobscot River. But even that prohibition might not be sufficient. In its 2004 report, the National Research Council (NRC, 2004) discussed the risks of fishing for (introduced) brown trout in salmon rivers, because brown trout are often confused with Atlantic salmon. It was pointed out that "[a]ny fishing that might take a wild Atlantic salmon constitutes an additional risk to the species." However, it was also recommended to reconsider regulations (size limits) for brown trout such that the established size limits for that species are large enough to protect salmon smolts and small enough to protect adult returning salmon; in other words, it should be illegal to kill trout as small or smaller than Atlantic salmon smolts or as large as adult Atlantic salmon. Thus, in considering C&R for endangered species, it is necessary to consider the effects of C&R (as well as fishing that takes some fish) on other species that occur in the same waters as the endangered species. As noted above, Maine implemented a limited C&R season for Atlantic salmon in the Penobscot River, where the fish are not listed as endangered; the Alantic Salmon Federation (ASF) issued a press release supporting the action because "it will rekindle the conservation spirit, and support local salmon clubs and other affiliates of ASF's Maine Council in their work towards clean, free-flowing rivers and healthy fish populations" (ASF, 2006).

There is also a question whether C&R is compatible with no-take reserves (Bartholomew and Bohnsack, 2005). Since there is some mortality associated with C&R, then it is incompatible with a strict no-take area (see discussion of endangered species above). But certainly, C&R might be a valid activity in many otherwise protected areas, and, certainly, C&R can be compatible with the generic conservation goals of no-take zones, if carefully monitored and implemented by anglers (Cooke et al., 2006). It would not be compatible with a non-consumptive reason for establishing a no-take zone, i.e., an area where ecosystems can function and develop as free as possible of human influence, or as a place where biota are protected from the effects of all human activities, which happens to include recreational fishing.

As this review has shown, there is a great need to better understand C&R behavior of anglers; the biological downsides of C&R, particularly at the level of populations and for the fitness of the individual fish; and the social norms that govern how different societies and cultures view and approach C&R. However, from the angler's point of view, there already is enough information available to improve C&R; for example, if undersized, immature fish are to be returned. Cooke and Suski (2005) presented a suite of generalized guidelines for C&R that should extend across species. They were: 1) minimize angling duration, 2) minimize air exposure, 3) avoid angling during extremes in water temperature, 4) use barbless hooks and artificial lures/flies, and 5) refrain from angling fish during the reproductive period. If such principles are properly applied, C&R can help protect fish populations. Our results from this synthesis support those general conclusions but can be extended further to include adding caution about angling in deep water, suggesting that circle hooks may be favorable

over other hook styles, and that if fish are temporarily retained for any reason, water quality should be maintained. Although it is difficult to make definitive conclusions regarding the biological aspects of C&R, we conclude that we now have sufficient information to provide intelligent and scientifically justified guidelines for C&R. In due course, we expect that these will be refined and expanded. We also support the development of species-specific, regionally specific, or fisheries-specific guidelines that incorporate more detail.

However, in some jurisdictions and cultures, even the best science that improves survival of released fish and minimizes stress and injuries during capture may not be accepted because C&R is considered an unethical fishing practice that has to be avoided (such as in some areas in Germany). Such perspectives are likely to increase world-wide in the wake of an urbanized society that is increasingly separated from nature and thus susceptible to opinions and worldviews that do not accept consumptive interactions between humans and fish (e.g., animal liberation or animal rights concepts). It is unlikely that such streams would be successful in banning subsistence-like recreational fishing. However, as was shown in this article, these perspectives do not tolerate C&R angling, particularly for table-sized fish that can be harvested. Restraining the possibility to release fish, however, would reduce the options fisheries managers have to conserve and protect exploited fish populations and preserve quality fishing experiences. It is their role to pay attention to the whole social-ecological environment, including cultural and institutional transformations that determine if and when C&R can be an acceptable and efficient fisheries management tool.

This review has shown that there is not only hooking mortality involved when issues of C&R need to be discussed and implemented into management and conservation. It is our hope that the present work has highlighted the array of cultural, institutional, psychological and biological factors, and dimensions involved in such a "simple" issue such as C&R. If managers and other stakeholders integrate some of the aspects discussed in the present work, progress towards successful treatment of C&R might be enhanced.

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