

Why the whole is greater than the sum of its parts: A case for population-level management

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ABSTRACT

Catch-and-release regulations in recreational fisheries have been implemented for decades with the intention of allowing fishing while reducing fishing mortality. In addition, voluntary catch-and-release behaviors are increasingly common. Social and scientific interest in fish handling practices in catch-and-release fisheries as they relate to stress, reflex impairment, reproductive success, and mortality has been expanding. The scientific literature is now replete with studies that examine these issues, and they have become a fixture in the public discourse on angling. Scientists and anglers are making fishing regulation proposals and suggestions for fish-handling practices. The proximal intent of these recommendations is to reduce excessive stress or mortality on a per capita basis with a belief that the reduction ultimately has a positive effect on the population. Whether the proximal intent achieves population goals depends on several factors, including effort, population dynamic rates, and stock-recruitment dynamics. This perspective reviews the state of the science relative to a hierarchical framework of fishery population dynamics, with a call for fishery scientists to consider their scope of inference and assumptions relative to conservation and population management.

INTRODUCTION

Catch-and-release (C&R; releasing a live fish after capture) regulations have been effectively implemented in many fisheries (e.g., Mallet & Thurow, 2022). As a result of these successes, along with changing angling ethics, there has been increasing application of both voluntary and mandatory C&R practices (Arlinghaus et al., 2007). In many angling communities, C&R has become not just a popular choice, but also a moral imperative for the sustainable use of fishery resources. The efficacy of any fishing regulation or normative behavior, including C&R, depends on a variety of factors across multiple scales of biological organization. The proximate intent of C&R is that individual fish will survive capture events so that they might continue to contribute to the population and the fishery. The ultimate intent of C&R is that the regulation or behavior will lead to improved population characteristics, including size structure and sustainability. The goal of this essay is to offer support to the perspective that only the ultimate intent, at the population scale, is relevant to fishery management as a regulatory construct.

Although C&R behaviors are intuitively expected to improve fishery sustainability, counterintuitive and undesir-

able fishery responses have also occurred, such as declining size structure (Sass & Shaw, 2020) or reduced participation. Despite mixed and complicated outcomes from the implementation of C&R practices, some, often very avid, anglers and fishing organizations lobby for restrictive harvest regulations and promote C&R ethics. In North America, fish populations are managed in the context of the public trust doctrine, where public desires for recreational fisheries inform management goals and objectives. The role of trust managers (i.e., management agencies) is to provide sound biological information and recommendations to trustees (i.e., commissions) and to enforce fishing regulations in congruence with angler desires while meeting trust obligations for all trust beneficiaries (i.e., the public) by providing sustainable fishing opportunities (Smith, 2011). Regulations might dictate where fishing is legal, when anglers are allowed to fish, which species and sizes of fish may be harvested, what types of tackle can be used, and how many fish may be harvested.

Science-based fishery management is best practiced with a broad understanding of biotic and abiotic factors that drive population dynamics, trophic dynamics, and ecosystem capacity, as well as the nature of the fish assemblage and associated

inter- and intraspecific interactions (Hubert & Quist, 2010). At the most fundamental level, management agencies must understand population dynamic rates to appropriately assess the need for regulations. Rates typically monitored by agencies include growth, recruitment, and mortality (both fishing and natural mortality), which, along with system capacity, define a population's capacity for production, yield, and replacement (Ricker, 1975). Additionally, agencies often monitor fishery-dependent metrics (e.g., exploitation) to understand harvest and fishing mortality. Managers then weigh the role of fishing mortality in the context of other dynamic rates to determine whether fishing-associated mortality represents a biologically significant limiting factor for the population or prevents attainment of fishery objectives (e.g., catch rates, size structure, yield; Allen & Hightower, 2010). If it does, then adjustments to regulatory structures may be warranted and a shift to more restrictive regulations like C&R might be required to sustain both fish populations and fishing opportunity. It should be noted that implementing regulations more restrictive than necessary or without adequate population-level justification may lead to managers losing credibility, unnecessary conflict among stakeholder groups and fish and wildlife management agencies, marginalization of consumption-oriented and casual anglers, or reduced participation.

Regardless of the nature of regulations, recreational fishing is a consumptive activity. All types of angling result in some fish mortality, including C&R angling. Concurrent with the rise of C&R fishing has been a growing body of literature evaluating attributes of angling (e.g., equipment, angler behavior) and the influences of those attributes on angled fish that are released after capture (e.g., Cook et al., 2015; Muoneke & Childress, 1994). These studies have evaluated factors, including, but not

limited to, hook design, bait or lure type, barotrauma, fishing during extremes of water or air temperatures, exposure to air during the handling phase of a C&R event, and post-release fish behavior and fitness. Nearly all these studies have evaluated the response(s) of individual fish by measuring physiochemical stress responses, reflex impairment, post-release predation, or other forms of immediate and delayed mortality. At a basic level, these studies seek to answer one of two questions. First, at what frequency do C&R fish die? Second, what are the relative consequences of C&R factors on individual survival? Both questions have been primarily investigated at an individual scale of biological inquiry. In other words, publications on this topic have been almost exclusively based on study designs that were only capable of improving understanding of the possible consequences to individual fish. However, as described above, management agencies generally require population-level justifications for implementing regulations because sustainability, viability, and production are population-level objectives. As such, fundamental angling-related research questions are most appropriate when conducted at the population-scale of inquiry and focus on (1) what proportion of the population dies from fishing, and (2) does fishing influence recruitment dynamics in a population and to what degree? At a population-scale, these questions remain the same whether a fishery is managed with C&R, or for high harvest and yield, or something in between. We are not the first to voice concern about appropriate scales of investigation and inference. In a call to action, Kerns et al. (2012) asserted that assessments of C&R mortality should be evaluated at the population level. They described population-scale fishing mortality (classically described as F ; Ricker, 1975) attributable to C&R as F_c , as a juxtaposition to the post-release individual mortality rates that are frequently described in the primary literature.



Photo Credit: Matthew Corsi

Certainly, the rate at which individual caught-and-released fish die is a critical piece of information for understanding population-level fishing mortality. Despite this importance, individual mortality is largely irrelevant for making informed management decisions without additional higher-level context. Therefore, the specific objective of this perspective is to place individual-level evaluations of C&R angling in the context of population-level dynamics and call attention to assumptions and conclusions that are often made outside the scope of inference with such evaluations. We use a simple framework to describe these questions in the context of angler attributes, potential responses of fish to angling events, factors associated with how individual responses scale to population-level rates, and the complex dynamics that drive the inter-generational variability in recruitment and productivity. Finally, we provide an argument for why it is appropriate to make recommendations for regulations and fishery management based on a population level of inquiry and inappropriate using an individual level of inquiry. Our perspective serves as a critique of arguments outlined in [Cooke et al. \(2025, this issue\)](#) and we invite the attention of readers to that paper and to [Corsi et al. \(2025, this issue\)](#), which attempts to identify areas of agreement and provide a path forward.

BIOLOGICAL SCALES AND MANAGEMENT

Most fisheries scientists are familiar with the importance of spatial and temporal scale in scientific inquiry. However, the concept of biological scales is also central to scientific inquiry and scope of inference relative to fisheries management. Standard biological scales include the Biosphere at the highest level, and sequentially nested within the Biosphere are ecosystems, communities, assemblages, populations, individuals, groups of cells, cells, and molecules. In recent decades, fisheries and aquatic scientists have increasingly considered ecosystem-scale management, and at the other end of that spectrum there have been concurrent advancements in physiology and genetics. As such, there is an argument for the inclusion of multiple biological scales in fisheries-related research and management. Because fish are mortal, and mortality can result from various sources, it follows that management for purposes of viability, sustainability, or conservation requires a multigenerational perspective focusing on recruitment, thereby suggesting that the *population* is the primary and appropriate scale for management.

A FRAMEWORK FOR CATCH-AND-RELEASE ANGLING

For the purposes of this perspective, we consider and discuss evaluations of C&R angling at the individual scale and identify factors for inclusion in evaluations so that they have relevance at a population scale ([Figure 1](#)). In the context of C&R angling, individual fish experience various stressors, primarily related to hooking injuries, physical exertion from fighting, and factors associated with handling. The relative effect of each stressor may be influenced by environmental conditions (e.g., water temperature). Each stressor is fundamentally related to angler behavior, choices, and motivations ([Arlinghaus et al., 2007](#)). Often,

fishery type influences the choices made by an angler (e.g., tackle, landing method), as well as the overall nature of the C&R experience for the fish. For example, effective fishing for Flathead Catfish *Pylodictis olivaris* in a Midwestern river requires different techniques than for Rainbow Trout *Oncorhynchus mykiss* spp. in a small western stream. Considering these examples, the experience of caught and released Flathead Catfish and a Rainbow Trout also differs given the divergent ecology of the species, different habitats, and constraints on handling (e.g., ability to be netted), among other things. Even within a fishery, a diversity of techniques may be used to capture fish and are often correlated with angler avidity, affinity for certain techniques (e.g., dry-fly fishing, setlines), interest in harvesting fish, and angling background or experience.

Nearly all studies indicate that the single largest stressor and mortality source is injury associated with hooking location and associated organ injury or bleeding. The nature of hooking injuries has frequently been related to hook type and bait type. Studies have compared the nature and rates of injuries for single vs. treble hooks, barbed vs. barbless hooks, circle vs. J-style hooks, and artificial lures vs. bait (e.g., [Meka, 2004](#); [Muoneke & Childress, 1994](#); [Schill, 1996](#)). Deep hooking rates, release times, and post-release mortality rates have been the primary metrics of interest in these studies.

Although choices of tackle and angler motivations have been associated with injury severity and fight time, which in turn influence stress responses, environmental conditions and handling practices also influence fish during a C&R event. Several studies have reported on factors associated with fish handling, such as the effect of net characteristics (e.g., material; [Barthel et al., 2003](#)). The literature is particularly replete with studies that address the length of time that fish are exposed to air during handling (e.g., [Cook et al., 2015](#); [Roth et al., 2018](#)), but most studies demonstrate limited mortality rates at typical air exposure times (e.g., [Twardek et al., 2018](#); [Whitney et al., 2019](#)). Potential “stress multipliers” like warm water temperatures have also been studied ([Boyd et al., 2010](#)), although the negative relationship between water temperatures and catch rates may ameliorate mortality in coldwater fisheries ([McCarrick et al., 2019](#); [Meyer et al., 2022](#)).

Regardless of mediating factors or in situ angler behaviors, documentation of individually based mortality rates by a litany of studies has focused attention and scrutiny of scientists, managers, and anglers on the potential for population impacts in C&R fisheries. However, this scrutiny typically fails to properly account for two critical and related factors that determine whether fishing mortality is important at a population scale. The first factor is the magnitude of angler effort in the fishery, which varies across time and space according to fishery quality, popularity, conditions, and the nature of the fish population being targeted by anglers. The second is catchability (the proportion of the population caught per unit effort). The product of effort and catchability is the probability that any given fish will be caught. Effort and catchability are functions of angler behavior, skill, regulations, prey availability, season, conditions, fish abundance, size structure of the population, and the nature of fish distributions. All of these elements and more influence $F_{c,r}$, which, in addition to any mortality attributable to harvest (F_h), determines total fishing mortality (F).

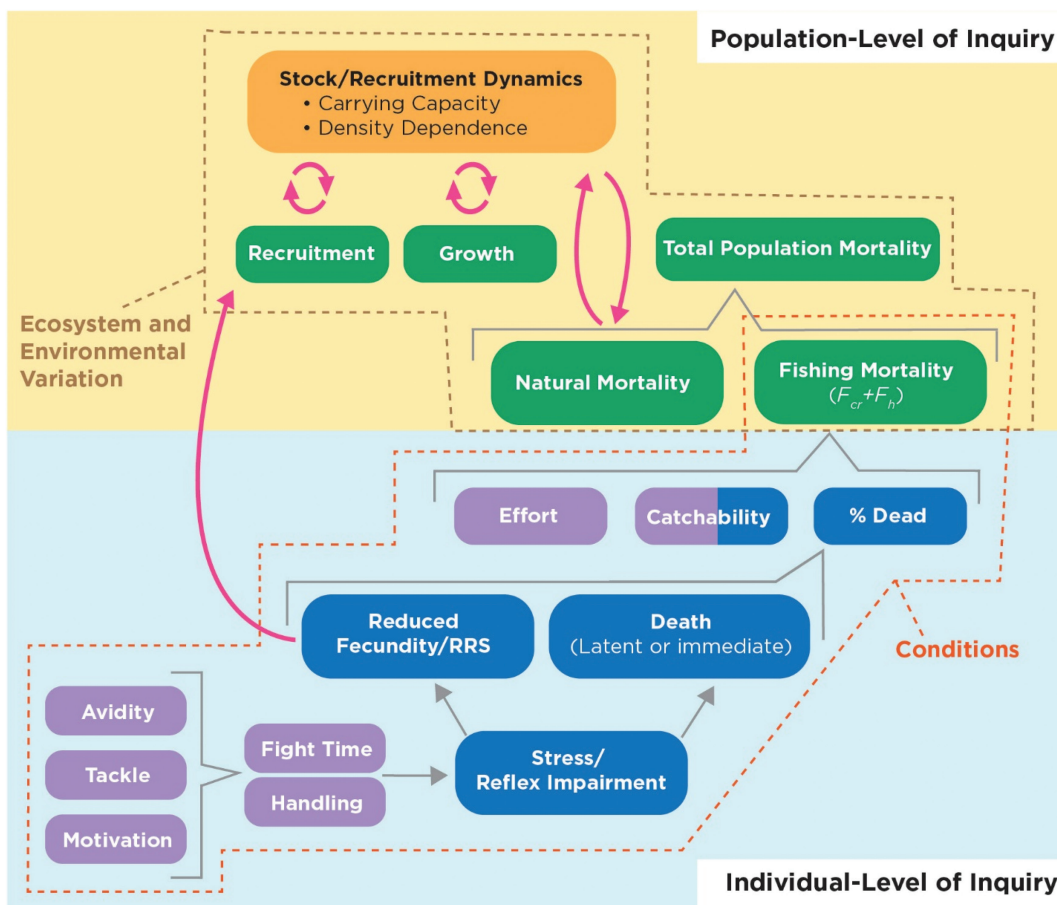


Figure 1. Conceptual model of processes associated with fish population dynamics within the context of a catch-and-release fishery. Processes and rate functions in the upper portion of the model represent those that occur at the population level. Factors in the lower portion of the model represent those related to the experience of an individual fish to a catch-and-release event. Factors in purple bubbles represent attributes of anglers. Processes in blue bubbles represent responses of individual fish to angling. Processes in green bubbles are population-level dynamic rate functions. The orange bubble represents multigenerational drivers of stock-recruitment dynamics. RRS = relative reproductive success. Conditions are a myriad of weather, hydrologic, water quality or other factors that can influence fishing for both anglers and fish, including effort, catchability, and stress responses. Ecosystem and environmental variation represent the interconnected complex of biotic and abiotic factors that drive population dynamics in fishes.



Photo Credit: Matthew Corsi

Of course, it is critical to understand the role of F in the dynamics of a fish population as it is a component of total mortality (Z). Also, it is important to understand the concept that F can be additive or compensatory to natural mortality (M). Additive mortality would assume an increase in F would lead to a concomitant increase in Z . However, this is often not as simple as it would seem because fish that die from fishing may have died anyway from natural causes during any given time interval or because reduced densities that are a result of F can lead to compensatory responses in M (Allen et al., 1998; Allen & Hightower, 2010; Ricker, 1975). Additive fishing mortality might be expected in populations with low densities or in populations with characteristically low rates of natural mortality (e.g., White Sturgeon *Acipenser transmontanus*).

Population conservation concerns related to C&R mortality stem from assumptions that fishing mortality is additive. Although fishing mortality may be completely additive, or nearly so, in some situations (Kerns et al., 2012), evidence suggesting that fishing mortality is additive is generally lacking. Even if fishing mortality is additive, increased mortality does not necessarily spell doom and gloom for a population. Growth and recruitment are also dynamic rates that have been shown to be density dependent (Ricker, 1975). So, even if the standing stock of a population is reduced, this can lead to better conditions for recruitment. Fish often grow fast at lower densities, thereby leading to higher fecundity, better egg quality, and reduced nest–redd competition. It should be noted that several authors have described the potential for reduced relative reproductive success resulting from C&R stressors (e.g., Bouchard et al., 2022; Richard et al., 2013; but see Roth et al., 2019; Whitney et al., 2019). However, even if reduced spawner abundance or reduced relative reproductive success leads to reductions in the number of eggs or emergent larvae, juveniles might experience higher growth and survival as a result of reduced intraspecific competition. Stock–recruitment dynamics are highly complex because of synergies among density, natural mortality, and growth. Furthermore, it is important to recognize that these dynamics play out within the context of ecosystem and environmental variation. In short, it is a complicated, but necessary endeavor to determine whether both F_{cr} and F_h are constraining to the age and size structure and productive capacity of a fish population; the conclusions of many individual-based studies make implicit assumptions about all of these complex factors.

APPROPRIATE BIOLOGICAL SCALES FOR MANAGEMENT

Our purpose with this perspective is to call attention to the overwhelming complexity of population dynamics and to emphasize the need for better research questions and study designs that focus on (1) what is the population-scale fishing mortality rate in a fishery with C&R regulations, and (2) does the magnitude of fishing-related mortality cause population declines or changes in structure? Our intent is not to

state that fishing mortality cannot lead to negative consequences in a fishery. For instance, growth overfishing (Allen & Hightower, 2010), changes in genetic structure (e.g., life history expression; Theriault et al., 2008), and alterations in age and size structure (Isermann & Paukert, 2010) are all potential negative consequences of fishing that may not necessarily result in a decline in abundance. Our purpose is to call attention to the numerous assumptions that must be made to arrive at the conclusion that C&R-associated stress and mortality undermine the effectiveness of C&R regulations and behaviors. The multilayered and synergistic factors that determine outcomes of any conservation activity require a population level of inquiry to have an appropriate scope of inference. Empirical, experimental, and modeling evaluations at the population level certainly come with their own sets of assumptions, but there is expectation to address those assumptions when communicating results to the scientific community (e.g., publishing in the peer-reviewed literature) and governing bodies (e.g., commissions). We find it concerning that many studies focused on fishing-related stress responses, relative reproductive success issues, and C&R-associated mortality use population conservation arguments to justify the study and make management recommendations at a population level, which, we argue, is often outside the respective study's scope of inference. For example, the vast majority of studies focused on air exposure of fishes (i.e., a subset of the C&R literature) have evaluated the effects of C&R at an individual level. This is not inherently problematic; after all, it is the individual that we measure, tag, and poke and prod during our research and monitoring activities. The concern is that most of the studies make implicit or explicit recommendations on population-level management that is well beyond the inference space of their work (e.g., Bieber et al., 2019; Logan et al., 2019; Schreer et al., 2005; Twardek et al., 2018). Even if the focus of these studies is about welfare and ethics, it is misleading to use *population* conservation as the justification for, or intended objective of, these considerations. In contrast, comparatively few studies have made population-level recommendations and evaluated effects at a population level (e.g., McCormick et al., 2021).

It is obvious that anglers, especially avid ones, place great importance on doing everything possible to maximize the survival of any fish they catch, handle, and release. Therefore, we appreciate how individual-based assessments of C&R mortality have informed and elevated ethical discussions about fish handling and better defined a conservative set of practices designed to give individual fish the best chances of post-release survival, which is indeed the objective of C&R at an individual-fish-level. Though we think it reasonable that best practices continue to be encouraged through a variety of means and media, elevating best practices to enforceable regulations seems to be a questionable use of the regulatory powers of state or provincial governments, in most cases, given the lack of population-level relevance. Instead, we suggest that it would be more appropriate to communicate best practices to anglers as suggestions and encourage such practices through a variety of educational and outreach efforts.



Photo Credit: Michael Quist

Unfortunately, confounding individual-based C&R mortality with population-level effects has had negative consequences and such studies have given anglers (and even many biologists and managers) a false, or at least untested, sense of the importance of C&R mortality in fisheries management. Recently, many anglers and others have lobbied for increased regulations related to improvements in C&R practices with the intention of conservation improvement, regardless of whether fishing mortality is a limiting factor. Given the myriad of more important factors at play (e.g., habitat alteration, interactions with nonnative species, barriers to movement), implementation of these sorts of regulations are unlikely to lead to more abundant populations or better size structure in many situations. Furthermore, connecting reductions in C&R mortality to conservation gives anglers a powerful sense of personal agency and purpose to control conservation outcomes. This is not a problem, per se, but the targets of angler political energy and spending become misaligned with factors that are far more likely to be limiting

for a population. Management agencies and commissions are frequently lobbied by anglers to regulate fish handling, to close fisheries during periods of warm water temperatures, or to restrict the types of tackle that are allowed in certain fisheries. Of course, these requests (especially tackle restrictions) might be a purely social issue related to one faction of anglers seeking greater exclusivity or a certain experience, but they are often justified as conservation endeavors. Agencies might surrender to these requests, or they might be reluctantly forced into using limited time, money, and human capital to conduct studies to evaluate the biological basis for these requests, even when those evaluations are very unlikely to conclude that fishing is a limiting factor. Indeed, meeting management objectives, such as desirable size structure, may become more difficult as C&R practices increase (Sass & Shaw, 2020). We argue that angler, scientist, and agency focus on this topic has become counterproductive and led to significant conservation opportunity cost. How would the productive capacity and sustainability of

many fisheries change if those anglers instead used their energy and voices to push for improvements to fish habitat or reconnection of migratory corridors? How would fisheries conservation benefit from more anglers focusing on the deleterious impacts of illegal fish introductions and a changing climate? Human opportunity costs are also critical to consider. As resource managers, and members of recreational angling communities, we have noted frequent examples of public shaming on the water and in social media as many C&R enthusiasts have adopted an almost religious adherence to handling best practices and fervent abhorrence of harvest. Even Guckian et al. (2018) highlighted the willingness of anglers to sanction other anglers' perceived bad behavior and state that "Most anglers simultaneously expressed a strong desire to sanction others in the future." Moreover, they state how peer sanctioning has a "significant and underappreciated role" in biological conservation. How many potential resource advocates have been shamed away from fishing due to one of these negative interactions with fellow anglers? We recognize that restrictive or complex regulations (e.g., C&R, no live bait, fly fishing only) alienate certain anglers and cause others to abstain completely from many fisheries (e.g., Johnston et al., 2011). How would alienation be exacerbated if an angler (novice or otherwise) was cited for holding a fish out of water for "too long" to capture a prized photograph of their catch? The direct interactions that people have with fish in a C&R event are integral to the fishing experience. The erosion of these interactions based on flawed logic about the relationship between fish handling and population dynamics represents irresponsible fishery management.

In conclusion, we call for scientists who are working at the individual fish or angler level of the framework described above to reconsider their true scope of inference and assumptions relative to conservation and population management. We certainly encourage more research on the impacts of C&R angling practices at a population scale but suggest focusing on populations for which C&R mortality has some practical likelihood of being a population-level limiting factor. Although estimation of the proportion of caught-and-released fish that die as a result of that fishing is not a population-scale metric, we fully recognize that F_{cr} (population-scale fishing mortality in a fishery) could be an important factor in fisheries where life history or low density provide conditions for mortality to occur in a manner that is potentially limiting to conservation goals. Regardless of that potential, we argue that it is inappropriate scientific practice to make recommendations when there is a clear mismatch between the biological scales of management and inquiry.

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