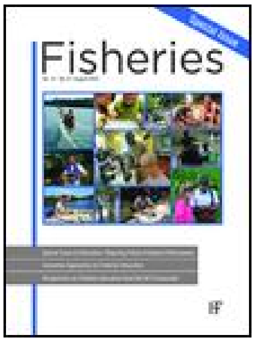

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FEATURE

Understanding and Managing Social–Ecological Feedbacks in Spatially Structured Recreational Fisheries:

The Overlooked Behavioral Dimension

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Recreational fisheries are empirically tractable examples of social–ecological systems (SESs) that are characterized by complex interactions and feedbacks ranging from local to regional scales. The feedbacks among the three key compartments of the recreational fisheries SES—individual fish and populations, regionally mobile anglers, and regional and state-level fisheries managers—are strongly driven by behavior, but they are poorly understood. We review and identify factors, antecedents to behaviors, and behaviors most important to the outcomes of the coupled SES of recreational fisheries, which emerge from a range of social–ecological interactions. Using this information, we identify data gaps, suggest how to reduce uncertainty, and improve management advice for recreational fisheries focusing on open-access situations in inland fisheries. We argue that the seemingly micro-scale and local feedbacks between individual fish, fish populations, anglers, and managers lead to the emergence of important macro-scale patterns—some of which may be undesirable, such as regional overfishing. Hence, understanding the scale at which the behavior-mediated mechanisms and processes identified in this article operate is critical for managing for the sustainability of spatially structured recreational fisheries. We conclude our study by providing relevant research stimuli for the future.

Comprensión y manejo de la retroalimentación socio-ecológica en pesquerías recreativas espacialmente estructuradas: la dimensión desapercibida del comportamiento

Las pesquerías recreativas son ejemplos de sistemas socio-ecológicos (SSE) maleables que se caracterizan por poseer interacciones complejas y procesos de retroalimentación que van desde la escala local a la regional. La retroalimentación entre los tres compartimentos principales de los SSE—peces como individuos y poblaciones, pescadores que se mueven en un región determinada y manejadores de pesquerías a nivel estatal—es gobernada por un componente conductual, sin embargo esto no ha sido bien estudiado. Aquí se revisan e identifican los factores, antecedentes del comportamiento y los propios comportamientos más relevantes con respecto al acoplamiento de los SSE en pesquerías recreativas; factores emergen a partir de distintas interacciones socio-ecológicas. Mediante esta información, se identifican huecos de información, se sugiere cómo reducir la incertidumbre y se mejora la asesoría para el manejo de pesquerías recreativas, particularmente en pesquerías continentales de acceso abierto. Se argumenta que la aparente microescala y retroalimentación local entre peces, poblaciones, pescadores y manejadores, dan como resultado importantes patrones de macroescala –algunos de los cuales son indeseables, como la sobrepesca. Por consiguiente, comprender la escala en la cual operan los mecanismos y procesos que controlan el comportamiento identificados en esta contribución, es un aspecto clave para el manejo de la sustentabilidad de las pesquerías recreativas que están espacialmente estructuradas. Se concluye el estudio presentando estímulos para la investigación futura que es relevante en este campo.

Comprendre et gérer les commentaires socio écologiques dans le cadre de la pêche récréative spatialement structurée: la dimension comportementale négligée

La pêche récréative est un exemple de systèmes socio écologiques (SES) qu'il est possible d'exploiter, qui se caractérisent par des interactions et rétroactions complexes allant de l'échelle locale à l'échelle régionale. Les commentaires entre les trois compartiments clés des SES—des différents poissons et des populations, des pêcheurs régionalement mobiles, et des gestionnaires de pêcheries régionales et nationales—sont fortement influencés par les comportements, mais souvent mal compris. Nous passons en revue et identifions les facteurs, antécédents de comportements, et les comportements les plus importants pour les résultats des SES associés de la pêche récréative, émergeant à partir d'une gamme d'interactions socio écologiques. Partant de ces informations, nous identifions les lacunes dans les données, suggérons la façon de réduire l'incertitude, et d'améliorer les conseils de gestion pour la pêche récréative axée sur des situations d'accès libre à la pêche continentale. Nous soutenons que les évaluations apparemment à micro-échelle et locales entre les différents poissons, les populations de poissons, les pêcheurs et les gestionnaires conduisent à l'émergence d'importants modèles à macro-échelle—dont certains peuvent être indésirables, tels que la surpêche régionale. Par conséquent, la compréhension de l'échelle à laquelle les mécanismes et les processus activés par les comportements identifiés dans le présent document opèrent est essentielle pour la gestion de la durabilité de la pêche récréative spatialement structurée. Nous concluons notre étude en fournissant des stimuli de recherche pertinents pour l'avenir.

INTRODUCTION

Recreational fisheries constitute the dominant use of many inland water bodies globally and generate substantial economic, social, and cultural values (Arlinghaus and Cooke 2009). Recreational fisheries can directly impact fish populations, and these impacts can sometimes lead to overharvest or even population collapse (Post et al. 2002). To prevent undesirable outcomes, the actions of anglers are generally constrained by management regulations, which are largely set by governance actors (commonly referred to as "managers") and further affected by informal norms of proper behavior (Cooke et al. 2013). Recreational fisheries are characterized by complex interactions between people and the natural environment, and hence constitute prime examples of coupled social–ecological systems (SESs; Arlinghaus et al. 2013). Social–ecological systems are defined as unique biogeographical physical units that are linked with, and affected by, associated human actors and institutions (Berkes and Folke 1998; Berkes et al. 2003; Ostrom 2007, 2009). System outcomes within recreational fisheries, such as regional-level overfishing patterns, strongly depend upon the configuration of interactions, processes, and feedbacks between the three main components of any recreational fishery: individual fish populations (composed of individual fishes), regionally mobile anglers, and regional or state-level managers (Arlinghaus et al. 2013; Hunt et al. 2013).

As coupled SESs, recreational fishery outcomes depend on both states and behaviors of each component—fish, anglers, and managers (Arlinghaus et al. 2013; Fenichel et al. 2013; Hunt et al. 2013). Behavioral processes among anglers and ecosystems can foster biological impacts on fish populations (e.g., declining sizes in catch), which in turn both affect and motivate responses from anglers and managers across spatial scales (Figure 1; Arlinghaus et al. 2013; Hunt et al. 2013). Therefore, the behavioral feedbacks between fish, anglers, and managers must be considered to make reasonable predictions of SES outcomes, which is critical for informing management

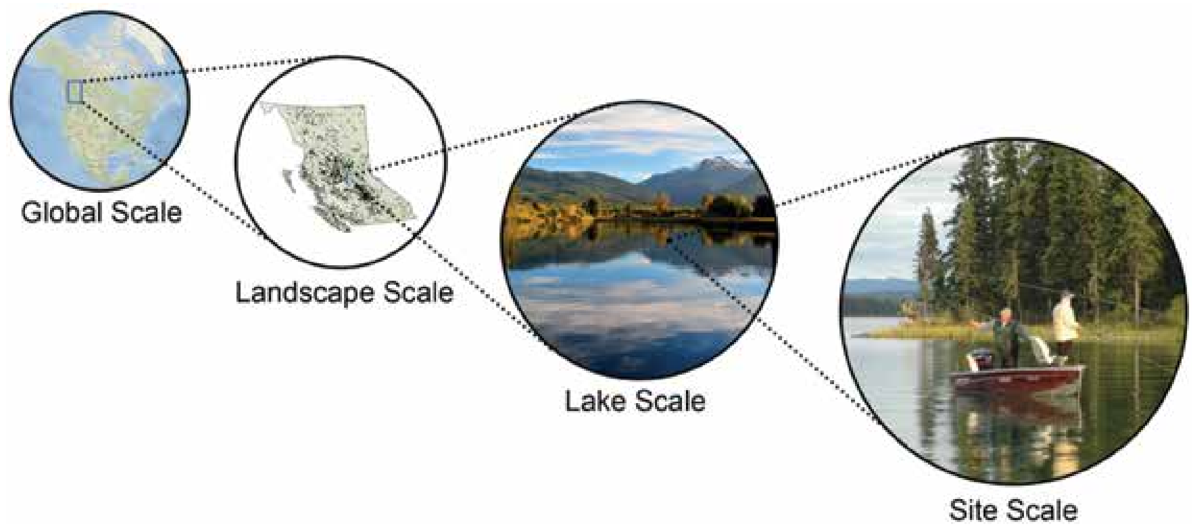

Figure 1. Recreational fisheries can affect social–ecological outcomes across a wide range of spatial scales. For example, at the global scale, changes in socioeconomic conditions can affect angler participation, whereas at the site scale, anglers may locally deplete fish populations. Conversely, changes at the site scale will have an effect at the regional scale by shifting angler effort.

decisions (Walters and Martell 2004). Specifically, there are three two-way behavioral feedbacks among fish, anglers, and managers that must be understood to determine outcomes of the SES of recreational fisheries (Figure 2).The behaviors of each of these three main actors affect each other and are reciprocal (e.g., the behavior of individual fish impacts anglers, and the behavior of anglers impacts fish). Given the complex nature of the resulting processes, it is important to understand how the two-way feedbacks affect overall system outcomes.

Outcomes of a recreational fisheries SES are diverse and are often considered the objectives of fisheries management. Outcomes can relate to anglers (e.g., effort, catch, economic impacts, and angler well-being measures such as satisfaction), fish populations (e.g., changes in stock structure), and managers (e.g., legitimacy of chosen management strategy). Many of these outcomes are interdependent (e.g., biological sustainability of fish populations affects the social well-being of anglers; Johnston et al. 2010). When viewed through the lenses of the now popular framework for the analysis of the sustainability of SES first put forward in Ostrom (2007), and refined in a series of papers afterwards (Ostrom 2009; McGinnis and Ostrom 2014), macro-scale system outcomes such as regional overfishing (abbreviated by O; Table 1) are the result of 10 key interactions (e.g., harvesting, information sharing, lobbying, networking, monitoring, and evaluation; abbreviated by I) that humans induce in so-called focal action situations. Action situations are defined as the collection of social and environmental processes through which interactions lead to outcomes through processes and feedbacks (Hinkel et al. 2014); they come in many variants such as determination of collective choice or operational rules, appropriation (e.g., harvesting), provisioning (e.g., stocking), monitoring, and sanctioning. In any given action situation, multiple human-induced interactions leading to micro-level and ultimately macro-level outcomes at a dynamic equilibrium are involved. Studying action situations are of key intellectual interest in SES studies in general, but limited attention has been devoted to understanding the roles of specific interactions in driving system outcomes as mediated through feedback-based processes (Hinkel et al. 2014). To add to this growing body of literature, we take a behavior-based perspective and outline a series of behavior-related processes involved in, or emerging from, human interactions with fish and aquatic ecosystems. Through our approach we contribute to calls of Hinkel et al. (2014) and Schlüter et al. (2014) of focusing on processes and feedbacks inherent in interactions to learn how they shape system outcomes in action situations.

Behavioral processes among anglers and ecosystems can foster biological impacts on fish populations (e.g., declining sizes in catch), which in turn both affect and motivate responses from anglers and managers across spatial scales.

The majority of research focused on the behavioral component of fish, anglers, and managers within recreational fisheries has so far described the diversity of behaviors that exist (e.g., within angler populations) or has emphasized isolated patterns of interest (e.g., changes in catchability due to effort sorting; Ward et al. 2013). Certain behavioral processes within the SES of recreational fisheries are thus well studied, such as the impact of anglers' behaviors on fish populations (Fulton et al. 2011; Fenichel et al. 2013; Hunt et al. 2013), whereas others are not (e.g., the impact of anglers' behavior on management). Overall, there is ample uncertainty regarding the occurrence of specific behaviors in specific conditions, and there is a need to understand what behaviors are most important to study. The ultimate goal is to identify those behaviors that are critical to influence socially or ecologically relevant system outcomes and how they relate to the 10 interactions proposed by McGinnis and and Ostrom (2014) and Ostrom (2007, 2009).

Although it is now increasingly recognized that the behavioral component of recreational fisheries is important, very few behavioral processes are accounted for in setting recreational fisheries policies and management decisions (Arlinghaus et al. 2013). There is thus a need to synthesize

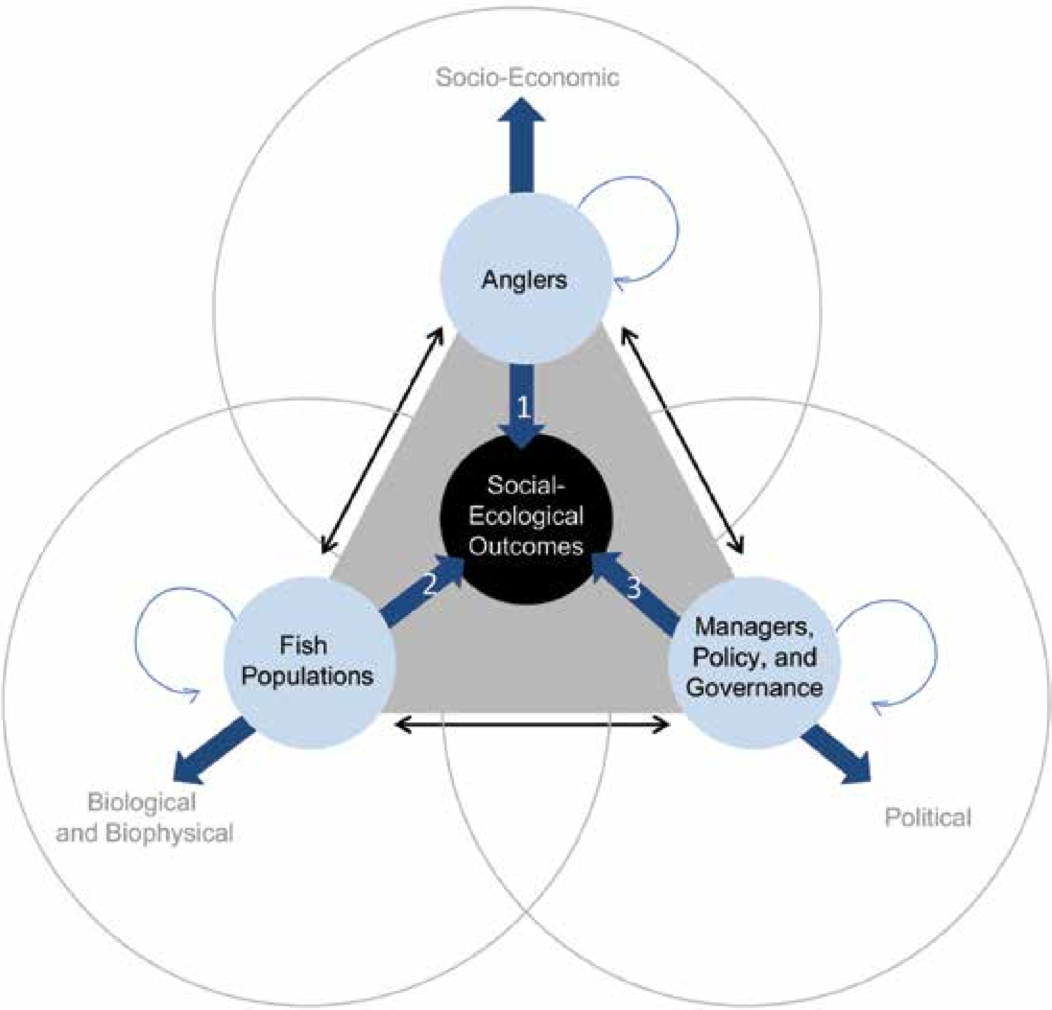

Figure 2. The direct and indirect interaction of fish populations, anglers, and fisheries managers within SES are nested within the broader social, economic, political, and ecological contexts. The arrowed numbers correspond to the three key processes, whereby actors influence SES outcomes and other actors: (1) fishing mortality and social well-being, (2) amount of compensation, and (3) choice and effectiveness of management strategy.

the literature describing relevant behavior-based processes and feedbacks to provide guidelines for where the greatest knowledge gaps remain and, most important, to understand what specific research and management actions can be employed to obtain behavioral information useful for informing management decisions. Rather than conducting a review of SES and recreational fisheries, the objective of this article is to identify factors, antecedents to behaviors, and behaviors most important to affect social, economic, and ecological outcomes of recreational fisheries. A further and more particular focus is to analyze the behavioral processes that operate in spatially structured open-access inland fisheries that are typical of North America and part of Europe (Daedlow et al. 2011). Specifically, we provide advice on how to reduce uncertainty and identify data gaps to improve the management of behavior-mediated processes in SES.

METHODS

A challenge of any integrated assessment of coupled SESs is the interdependencies among all components. To address the issue in our focal SES of recreational fisheries, we divided the overall system into smaller and more approachable components—fish, anglers, and managers. Then, we considered six distinct key behavior-driven processes and feedbacks among these components given their relevance for affecting system outcomes through human-induced interactions such as harvesting or monitoring (Figure 2):

1. How fish behavior affects anglers.
2. How fish behavior affects managers.
3. How angler behavior affects fish.
4. How angler behavior affects managers.
5. How manager behavior affects fish.
6. How manager behavior affects anglers.

Obviously any of these two-way feedbacks will exert effects on other components of the SES of recreational fisheries, but for the sake of tractability we decided to focus on two-way processes first. We then screened and synthesized the primary literature regarding behaviors of fish, anglers, and managers to identify some of the most common, important, and/or well-studied ways in which the behavior of one part of the system impacts another (Table 1). The purpose here was not to provide an exhaustive list of behaviors but rather to describe the common mechanisms that exist as part of the six-directional behavioral feedbacks and have potentially important implications for fisheries management and research. Based on

Table 1. A summary of pathways and drivers of the six key behavioral-based feedbacks within recreational fisheries, factors that may impact social–ecological outcomes, and the relationship to the 10 key interactions (I) proposed by McGinnis and Ostrom (2014) for SES in general.

Process relationship	Relationship to 10 key interactions (I)	Pathway/ driver	Factors that impact social–ecological outcomes	Key citations
How angler behavior impacts fish populations	I1 harvesting, I7 self-organizing activities	Attribute preference	Trade-off between catch and non-catch-related attributes Attachment to fishing sites Catch and harvest orientation Changes in resource and social conditions	Hunt (2005) Johnston et al. (2010) Hunt et al. (2011)
	I1 harvesting, I5 investment activities, I3 conflicts, I7 self-organizing activities	Personal constraints	Structural (i.e., limited resources, age, health concerns, lack of leisure time) Intrapersonal (i.e., perceived lack of fishing skills) Interpersonal (i.e., lack of social networks)	Fedler and Ditton (2000) Sutton (2007)
	I2 information sharing, I7 self-organizing activities	Learning and awareness	Information sharing Awareness of resource conditions Diffusion of information	Papenfuss et al. (2015)
How angler behavior impacts managers	I2 information sharing, I3 deliberation processes, I6 lobbying activities, I8 networking activities, I9 monitoring activities, I10 evaluative activities	Communication	Managers wishing to avoid complaints from vocal stakeholders	Little et al. (2004)
		Compliance with regulations	Awareness of regulations Strength of normative pressures Relative weight of formal and informal institutions (i.e., rules, norms, and strategies that guide interactions among anglers and fish)	Hunt et al. (2010) Miller et al. (2010) Johnston et al. (2015)
How fish behavior impacts anglers	I1 harvesting, I2 information sharing	Spatial and/or reactive behavior of fish to recreational fishing	Variability in vulnerability to angling due to learning or evolution of low-vulnerability genotypes	Klefoth et al. (2013) Matthias et al. (2014)
	I1 harvesting, I2 information sharing	Fisheries-induced evolution	Genetic change in life history traits and vulnerability to fishing	Heino et al. (2013) Laugen et al. (2014)
	I1 harvesting, I2 information sharing	Density-dependent vital rates	Growth, mortality, and recruitment Depensatory response in per capita growth rates	Hilborn and Walters (1992)
	I1 harvesting, I2 information sharing	Inter- and intraspecific competition and interactions	Effects of fishing on ecosystem stability Truncation of age and size-structure	Walters and Kitchell (2001)
How fish behavior impacts managers	I9 monitoring activities, I10 evaluative activities	Spatial behavior of fish	Density-dependent catchability as a result of habitat and/or behavioral aggregations	Ward et al. (2013)
		Vulnerability to sampling gear	Impacts the ability to monitoring fish populations	Alós et al. (2015)
How manager behavior impacts fish	I5 investment activities, I9 monitoring activities, I10 evaluative activities	Direct manipulation	Habitat and/or stock manipulations	Cowx (1994) Lorenzen et al. (2012)
		Choice of management strategy	Fishing regulations (i.e., size and/or bag limits) control size structure of fish population	Hilborn and Walters (1992)
How manager behavior impacts anglers	I2 information sharing, I3 deliberation processes, I4 conflicts, I7 self-organizing activities, I8 networking activities	Effectiveness of management strategy	Impacted by angler's awareness levels, preferences, competencies, perceptions of legitimacy, and expected penalties and perceptions	Sullivan (2002) Page and Radomski (2006) Walters and Martell (2004)

the available information, we identify some of the most critical uncertainties in each of the six feedbacks and suggest actions that one could undertake to help understand and incorporate these behaviors into management.

PATHWAYS AND DRIVERS OF SIX BEHAVIORAL FEEDBACKS

How Angler Behavior Impacts Fish Populations

Anglers' behaviors can have a profound impact on fish populations (Post et al. 2002). This occurs most directly through the anglers' decisions to fish and harvest their catch. Decisions on whether and how much to fish at the microscale of individual sites determine aggregate angler effort and its dynamics at the macroscale of regions (e.g., how much aggregate effort changes with fish abundance; Fenichel et al. 2013), which is directly related to fishing mortality through harvest or catch-and-release mortality (Hunt et al. 2011). Anglers' subsequent decisions about where and what species and size of fish to target for catch and harvest influence fish abundance and size/age structure (Lewin et al. 2006) and may even lead to the evolution of life history and behavior (Lewin et al. 2006; Alós et al. 2012). Angler behaviors related to fishing and harvesting decisions are strongly linked to their preferences (Hunt 2005; Abbott and Fenichel 2013) and realized satisfactions (Arlinghaus 2006) as well as situational constraints. Importantly, angler preferences, motivations, and perceived constraints are expected to be heterogeneous across fisheries and within a single fishery (Bryan 1977; Johnston et al. 2010; Ward et al. 2013) and even within a single angler over multiple fishing days (Beardmore et al. 2011).

Anglers' behaviors regarding information transfer can also impact fish populations indirectly by attracting or repelling effort (Little et al. 2004). Public information (e.g., via online forums, tackle shops, personal communication) may improve angler knowledge of where and how to fish (Papenfuss et al. 2015), to the point that anglers approach "perfect" knowledge of all fishing opportunities. Public knowledge transfer can lead to increased catchability (by attracting highly skilled anglers) and potentially increased fishing mortality. A key related angler behavior is how anglers choose to redistribute their effort across the landscape of angling opportunities through site choice behavior (Hunt 2005; Abbott and Fenichel 2013). The redistribution of anglers will impact regional fish populations and likely determine both the overall exploitation rate as well as potential for depletions of stocks near high latent effort agglomerations (Hunt et al. 2011; Post and Parkinson 2012).

Angler behavior can also directly impact fish populations from purposeful or accidental transplanting of nonnative fish or other aquatic organisms; for example, through bait buckets (Hickley and Chare 2004). Illegal stocking is now recognized as a substantial problem, because the introduced species may become established and markedly alter the ecosystem (Johnson et al. 2009). Similarly, anglers may inadvertently or purposefully alter fish habitat by translocating aquatic vegetation during fishing site construction, altering stream beds in particular forms of fishing (e.g., wading), or adding structural habitat as fish aggregating devices (e.g., brush piles; Lewin et al. 2006). These changes may impact the food web directly or indirectly by altering foraging and refuge habitats (Biggs et al. 2009).

How Angler Behavior Impacts Managers

Anglers may directly impact managers through available consultation processes where anglers voice their perspectives about the acceptability of different regulations governing the outputs (e.g., catch) and tactics (e.g., gear, equipment, seasons) legally permissible (Hunt et al. 2010; Miller et al. 2010). Compliance with management regulations can greatly influence the management of recreational fisheries and, in some instances, noncompliance can result in overfishing outcomes (Johnston et al. 2015). Research on the acceptability of regulations has shifted from focusing on single regulations to full evaluations of trade-offs among different regulations and corresponding outcomes because no regulation is perfectly able to meet both consumptive and nonconsumptive, trophy-oriented angler preferences (Hunt and Morgan 2005). However, although the relevance of angler typologies and angler preferences for the acceptability of harvest regulation is now well established (Dorow et al. 2010), very little research in recreational fishing has focused on studying how anglers influence the development of regulations in fisheries agencies.

How Fish Behavior Impacts Anglers

Fish behavior, including foraging strategies, schooling behavior, and habitat use, influences the vulnerability of fish stocks to anglers and thus influences angler catch rates (Askey et al. 2006; Erisman et al. 2011; Klefoth et al. 2013; Matthias et al. 2014). Fishes that school or those that aggregate on the best habitat have the potential to provide high catch rates to anglers even if overall fish abundance is low. Fish behavior and habitat use can be highly seasonal, with many species more vulnerable during spawning seasons as fish aggregate in predictable locations (e.g., river or shallow-water spawners, spawning shoals), which can further increase angler catch rates and catchability (Erisman et al. 2011). Thus, predictable fish behaviors may cause angler catch rates to improve spatially or temporally and increasing angler catch rates can result in increases in overall fishing effort. This provides one feedback loop for the effects of angler behavior on fish populations that is described above.

In addition to habitat use effects on angling vulnerability, fish that are caught and released may also have differential vulnerability as released fish may enter an invulnerable state for a certain period of time (Askey et al. 2006; Klefoth et al. 2013). Thus, fish may become relatively unreactive to fishing after being caught and released, and this change in behavior can directly reduce angler catch rates. Lower vulnerability to angling would also cause a decoupling between fish abundance and angler catch rate (Alós et al. 2015), indicating that strong movement of fish to the invulnerable state could substantially reduce angler catch rates (Cox and Walters 2002). Such effects are also conceivable in response to the selection of low-vulnerable phenotypes over time (Härkonen et al. 2014). However, few studies have evaluated to which degree different fish species can avoid capture or otherwise enter an "invulnerable" state after fishing and, thus, the effects of fish behavior on angler catch rates are unknown for most species.

How Fish Behavior Impacts Managers

Fish behavior directly impacts managers through the ways in which behavior might impair attempts to monitor fish stocks. For example, fish behavior influences vulnerability to sampling gears and gear selectivity and thus influences the ability of managers to effectively assess fish stocks (Alós et al. 2015). Monitoring programs often attempt to minimize bias in catches by standardizing sampling methods (Bonar et al. 2009), but uncertainty in fish behavior to sampling gears influences uncertainty in the management process. Fishery-dependent data such as creel survey CPUE data can be an ineffective index of fish abundance due to hyperstability caused by fish aggregating behavior (Ward et al. 2013), hyperdepletion caused by fish learning in catch-and-release fisheries (Alós et al. 2015), or variation in both angler skill and choices of where and when to fish (summarized above). Thus, fish behavior influences management through biases and variation in the observation and monitoring process. Understanding how fish behavior influences the selectivity of various sampling gears is therefore a critical management need for the future.

How Manager Behavior Impacts Fish

A direct way that behavior of fisheries managers influences fish is via stocking, including enhancing existing populations, restocking locally extirpated populations, or introducing new species to systems (Lorenzen et al. 2012). Fisheries managers stock hatchery-reared or wild fishes to increase fishery yield (either through manipulation of fish abundance and/or trophic interactions), aid in the reconstruction of imperiled and/or overexploited populations, and provide partial mitigation for the ecosystem effects of fishing (Lorenzen 2005). However, several authors have suggested that the decision of managers to stock fish often occurs with limited knowledge or consideration of the resulting ecosystem impacts (van Poorten et al. 2011) and stocking has resulted in severe consequences and unintended outcomes for the entire aquatic ecosystem (Knapp et al. 2001; Lorenzen et al. 2012). The other primary augmentative management strategy managers may choose to employ is habitat restoration, which potentially impacts the carrying capacity of the population (if habitat used during recruitment is enhanced/restored) or may also impact the spatial location and aggregations of fish (and therefore impacts catchability; Parkinson et al. 2004).

A less common manager behavior potentially impacting fish populations relates to how alternative management strategies are considered and evaluated for given fisheries. Risk-averse manager behaviors motivated by reducing exposure to critique by stakeholders can result in a bias toward inaction, which can potentially allow overfishing to continue to deplete fish populations (Walters and Martell 2004). Conversely, risk-prone managers who are motivated strongly to improve resources and stakeholder satisfaction may consider a wider range of alternative strategies and options, though this may come at professional risk of conflict by alienating certain stakeholder groups. Such managers are more likely to engage in active adaptive management, but no research exists on recreational fisheries linking personality traits of managers, cultural values of organizations, reward systems of managers, and management decision making.

How Manager Behavior Impacts Anglers

Managers most directly influence anglers through the use of input or output regulations. These decisions are related to the resources available and the existing legal and policy frameworks but are also a function of individual manager's behaviors/beliefs, particularly with regards to risk, the organization's general philosophy for management, and current policies (see above). Though regulations can focus on input controls such as limits to the number of anglers or total effort, most recreational fisheries use output-based regulations or gear restrictions to limit the effectiveness of angling effort. Output-based regulations such as size-based harvest limits and creel limits can alter anglers' harvesting decisions and even the total amount and distribution of effort for a spatially structured fishery (Beard et al. 2003) because of the potential conflicts of regulations with angler preferences (e.g., a consumptive angler would not fish a system where total catch and release is prevalent; Johnston et al. 2011). Other regulations are designed to influence the effectiveness of effort by altering when, where, and what anglers can target and the type of gear and equipment one can use while fishing. These regulations serve not only to indirectly protect fish stocks but can also affect the well-being of anglers (Johnston et al. 2010).

Risk-averse manager behaviors motivated by reducing exposure to critique by stakeholders can result in a bias toward inaction, which can potentially allow overfishing to continue to deplete fish populations.

Certain manager behaviors can indirectly impact anglers through changes to non-catch-related attributes such as the accessibility of fishing sites or the availability and quality of facilities (Hunt 2005). Moreover, broader societal-level developments change the general pool of anglers participating in fishing (Abbott and Fenichel 2013). How managers behave with respect to enforcement also impacts anglers, both through obvious direct linkages and indirectly by influencing the legitimacy of the regulations (Radomski et al. 2001; Cooke et al. 2013). This indirect route, by which manager behavior influences the perception of the fishery, is perhaps the most prominent impact on anglers given the large influence of informal institutions on angler behavior (Cooke et al. 2013).

KEY MANAGEMENT AND RESEARCH NEEDS

For each of the six behavioral interactions described above, we not only identify how they relate to the 10 key interactions proposed by McGinnis and Ostrom (2014) for SES in general, but we also outline some of the most critical uncertainties and suggest actions that could be undertaken (both in terms of research and management) to help understand these behaviors and incorporate this understanding into management strategies.

How Angler Behavior Impacts Fish Populations

- There is a need to empirically evaluate factors that control angler effort and quantify variability in the effort response as a function of target species, local fishing quality, and angler characteristics. Relatedly, it is important to understand how and how quickly anglers redistribute themselves across landscapes or across different fishing opportunities and/or target species. These needs can be best accomplished by measuring an actual response in effort to experimentally induced changes in resource conditions (e.g., Johnson and Carpenter 1994; Post et al. 2008), or by utilizing behavioral models to represent the underlying angler behaviors as they emerge from angler-type dependent preferences (Schuhmann and Schwabe 2004; Johnston et al. 2010; Abbott and Fenichel 2013; Fenichel et al. 2013).
- The population-level effects of discard-induced recreational fishing mortality (via catch-and-release angling) are largely unknown, although some simulation modeling studies exist (e.g., Johnston et al. 2015). Though most studies report a

proportion of hooking mortality, more rarely is the nominal fishing mortality rate (from catch-and-release angling) estimated. Knowing it will aid in modeling impacts of angler choices to release fish on fish populations.
- Technological advancements in communication of fishing information (from online forums to inexpensive GPS units to satellite imagery) may have dramatically changed catchability over time, but very few studies have tried to quantify such changes. Insights could be gained via swept-area calculations, as well as novel fishing experiments contrasting different levels of technology or information employed by participating anglers and different gear types used.
- Much human dimensions work has focused on the occurrence of multiple angler typologies, but less has focused on how researchers and managers can quickly assess angler typology across different fisheries in creel surveys. Rapid prototyping of anglers may be useful in prioritizing management strategies, and a spatially explicit understanding of typologies may be especially useful for regions where competing motivations (and typologies) exist that cannot be reconciled on individual fisheries (e.g., trade-off between maximizing yield and size of fish in the catch; Gwinn et al. 2015).

How Angler Behavior Impacts Managers

- There is a need to more fully understand angler desires because nearly all of the common methods that managers use to gauge angler opinions about management (e.g., advisory committees, open houses, e-mail commentary) are subject to strong bias by vocal minorities (Hunt et al. 2010). Therefore, the perspectives that managers hear from these methods may be the “squeaky wheel” rather than the “silent majority” (Hunt et al. 2014). Managers interested in equity may want to focus on obtaining a representative sample of anglers’ perspectives toward management issues. In particular, methods that identify trade-offs and challenge anglers to consider these trade-offs when making informed choices about management options are recommended.
- Few studies have examined behavioral factors that impact illegal harvest in recreational fisheries (e.g., Sullivan 2002), and research focusing on how compliance rates vary by regulations represents a common plea (Radomski et al. 2001). We suggest that researchers focus on understanding how compliance is realized in anglers and identify the strength of normative pressures on compliance and the relative weight of formal and informal institutions (defined as voluntarily agreed rules, norms, and strategies that guide interactions among people and the resource) in affecting compliance. The relationship between angler behavior and regulations can be explored by experimentally altering regulations and enforcement (Walker et al. 2007). Additionally, noncompliance with regulations might vary with angler awareness (Page and Radomski 2006). To overcome this awareness deficiency, there is a need to study the effects of different communication strategies and how these strategies affect the spread and acceptance of regulations by anglers. By quantifying angler noncompliance under various management scenarios and reducing noncompliance through outreach programs, managers can develop regulations that maximize angler satisfaction and reduce illegal harvest.

How Fish Behavior Impacts Anglers

- Quantifying how fish habitat use and aggregation propensity influence catchability (and thus angler CPUE) is potentially very important, yet evidence for it exists for few species. Telemetry data combined with high reward tagging could identify fish habitat use and vulnerability patterns across species and habitats. Such an understanding could help to predict angler effort responses to changes in species availability/vulnerability as well as individual vulnerability within populations at different locations and during different times of the year.
- There is a need to understand the degree to which fish learn to avoid capture and become invulnerable and the rates at which fish move between the vulnerable and invulnerable state. In addition, we need to understand the degree to which genetic selection for vulnerability-related behaviors might result in permanent alteration to catchability. This information is required for a range of species that support recreational fisheries.

How Fish Behavior Impacts Managers

- There is a need to quantify how fish habitat use and movements influence vulnerability to sampling gears so that managers can improve fish assessment methods using telemetry technologies.
- Spatial information on angler catch data can be used to identify the potential or hyperstability in angler catch rates (Walters and Martell 2004), and this enables managers to increase the utility of CPUE as an abundance index and, thus, the effectiveness of fisheries-dependent monitoring data. Conducting whole-lake experiments (e.g., Ward et al. 2013) using high-resolution tracking and fishing experiments is ultimately the best method to evaluate the potential for hyperstability and potentially of hyperdepletion in angler CPUE and/or density-dependent catchability.

How Manager Behavior Impacts Fish Populations

- It is important to understand how the spatial aggregation of fish is affected by habitat alterations (e.g., fish aggregating devices) as well as understanding how manager decisions impact fish as mediated by angler effort responses.
- There is a need to understand how much individual manager preferences for a given action affect system outcomes and how decisions are governed by multi-level influences related to agency philosophy and legal frameworks. Though the majority of research focuses on how various management strategies could impact fish and anglers, comparatively little is devoted to understanding how managers make decisions, despite the fact that this likely has an outsized impact on system outcomes.

How Manager Behavior Impacts Anglers

- A need exists to understand better how different recreational fishing regulations influence the tactical responses of anglers toward fishing. Most research on this topic has focused on hypothetical or intended responses of anglers to regulations or only on effort responses by anglers (Abbott and Fenichel 2013). Managers would benefit from carefully designed experiments that manipulate actual fishing regulations and observe responses from anglers beyond effort to changes in tactical responses such as gear and equipment choices, catch-and-release behaviors, and substitution among fish species.
- Another important need is to understand the effectiveness

of programs that are designed to recruit and/or retain individuals into recreational fishing, because promoting angling is often a key focus of many agencies. Again, experiments should be implemented to understand how managers can maintain or grow fishing participation rates and the well-being that individuals accrue from fishing.

- Angler hypothetical response to management behavior related to non-catch-related factors such as facilities improvement has outpaced empirical evaluations of actual responses. As a result, there is a need to document observed changes in angler well-being (e.g., satisfaction) following such improvements in non-catch-related aspects of fishing using revealed preference data (Abbott and Fenichel 2013).
- Understanding how management behavior may engender angler investment and responsibility for sustained fish populations and potential participation in the management itself is a challenge. Experimental inclusion of anglers in management processes has been documented, and such before–after comparisons with appropriate controls may be particularly useful in the future to measure how stakeholder attitudes/knowledge/actions are impacted by manager behaviors and by stakeholder involvement in deliberate processes.

DISCUSSION

The behavioral responses among fish populations, anglers, and managers relate to all 10 key interactions in SES identified by McGinnis and Ostrom (2014; Table 1),which in turn strongly drive social–ecological feedbacks and correspondingly influence a range of social–ecological outcomes (Johnston et al. 2010; van Poorten et al. 2011). Understanding sources of uncertainty that result from the behaviors of fish, anglers, and managers is thus critical for effectively managing recreational fisheries because these uncertainties can lead to unexpected outcomes within the SES (Carpenter and Brock 2004; Fulton et al. 2011; Arlinghaus et al. 2013). However, traditional management strategies for recreational fisheries have mainly focused on quantifying uncertainty in the biological response of fish populations to harvest (Hilborn and Walters 1992). This approach falls short in addressing the key behavioral feedbacks among the social and ecological subsystems that ultimately drive the system (Arlinghaus et al. 2013). In fact, evidence is mounting that understanding the uncertainty in the human response is of utmost importance when planning management regulations but is traditionally undervalued in fisheries science for a variety of reasons (Fulton et al. 2011; Fenichel et al. 2013; Hunt et al. 2013). We argue based on the evidence compiled narratively in this review that successful management of recreational fisheries within the SES requires understanding the strength of the social–ecological feedbacks between fish, anglers, and managers, which necessitates a focus on investigations of key behavioral factors in the SES, which in turn drive interaction quality and strengths among social and ecological compartments (Arlinghaus et al. 2013).

We have summarized approaches that managers and researchers can use to address areas of outcome uncertainty in key SES interactions leading to outcomes through a range of behavioral processes. Three main categories of knowledge gaps are evident. Firstly, there is a substantial need for research to understand how anglers respond to various factors—whether it is how angler behavior impacts fish or how manager behavior impacts anglers—as individuals but also as part of collectives (social groups). Though a lot of work has been done to study the antecedents of angler behaviors (e.g., attitudes), relatively little of this work appears to have influenced how management decisions are made. Therefore, more empirical observation studying angler responses will help to make the importance of angler behavioral processes apparent and lead to mechanistic models that can then be linked to population dynamical models (e.g., Johnston et al. 2015) in a spatial framework (Hunt et al. 2011). Secondly, fish catchability changes both in response to the act of angling (within the realms of plasticity and evolutionary change) as well as due to spatial changes caused by habitat modification (Askey et al. 2006; Ward et al. 2013). Because catchability is the direct link to fish population dynamics and the utility and (catch-related) satisfaction of anglers (Johnston et al. 2010; Ward et al. 2013), understanding the spatial and temporal dynamics of catchability as population-level metrics that aggregate individual-level vulnerabilities is critical. Thirdly, similar to anglers, managers are humans with complex and heterogeneous preferences and motivations, who are embedded in a complex nest of legal frameworks, agency policies, organizational cultures, and individual-level preferences. Decisions of management as a multi-level problem have not been studied at all, although they can have a substantial impact on system outcomes due to the influence that mangers have on regulations as well as on their interactions with stakeholders. The latter is particularly important because research increasingly suggests that the resilience of SES depends on engagement of stakeholders and the use of polycentric governance frameworks (Biggs et al. 2012).

The complex interactions, processes, and feedbacks in the SES of recreational fisheries require multipronged management strategies to address multiple objectives (Biggs et al. 2012). We recognize that context matters and factors external to the core SES of recreational fisheries (e.g., decisions about water management or agriculture) may impact processes in recreational fisheries in systematic and often uncontrollable ways (Figure 2; Hunt et al. 2013). Nevertheless, understanding the often overlooked behavioral processes inherent in the core SES can help foresee how the system might develop in response to external and internal changes. We also find that behaviors are embedded in all 10 key interactions driving SES dynamics in general (Table 1), which further supports the need for more research in this area. Many of the research directions we provide are cost intensive. Therefore, in times of diminishing funds dedicated to natural resource management, determining management and research priorities and the expected outcomes is important but can be done with just a few key structural changes as outlined by Hansen et al. (2015). To begin addressing this complexity, successful management of SES requires developing quantitative simulation models to predict the range of plausible responses of the system to both human- and non-human-induced changes (Binder et al. 2013). There is increasing recognition of the importance of integrated models that link social and ecological processes to understand dynamics in recreational fisheries (Hunt et al. 2011; Fenichel et al. 2013; Post 2013; Schlüter et al. 2014). We argue that a key part of this dynamic interaction includes behavioral feedbacks between fish, anglers, and managers, and these processes and corresponding uncertainty need to be explicitly specified in integrated models to be assisted by new empirical findings from properly conducted adaptive management approaches (Hansen et al. 2015).

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