Ecology for Understanding Recreational Fishers and Fisheries

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Abstract We examine recreational fisher behaviour and recreational fishery systems through the lens of an ecologist to understand the dynamical properties of these social-ecological systems. From the perspective of an ecologist, recreational fishers and the fish they capture can be viewed as analogous to predator-prey systems. Our understanding of predator-prey interactions is supported by a richness of empirical and conceptual research, primarily developed within sub-fields of behavioural, population, and community ecology. We develop this analogy between predator-prey ecology and fisher behaviour by examining the key underlying processes within a conceptual framework based on simple models. We then characterize several processes inherent to recreational fisheries that can, at least in part, decouple these simple predator-prey interactions. We examine the impacts on fisher behaviour and fishery outcomes of non-random spatial distributions of fishers and fish, heterogeneity of fisher behaviour, and multi-species fisheries, and develop an enhanced

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framework to understand these dynamic interactions. Population ecology and density-dependent feedbacks are important concepts underlying fish population dynamics, and also set limits to the sustainability of fisher harvest. Predator-prey theory is helpful in understanding fisher behaviour and its feedback with fish production, fishery quality, and sustainability. As fishers often prefer larger sizes in their catch, the predator-prey dynamic involves ecological concepts related to life-history theory and size-structured interactions. Although some recreational fisheries target a single species, many involve multi-species fisheries, such that food web theory is also important in understanding ecological feedbacks between fisher behaviour and fishery outcomes. In addition, individual recreational fisheries are typically embedded within landscapes of alternative fisheries, so the spatial configuration of fishing opportunities and the spatial behaviour of fishers is central in understanding fishery outcomes across landscapes. We discuss field methods used to measure fisher behaviour and provide empirical examples from well-studied recreational fisheries. Field methods to measure catchability, catch-per-unit effort, and landscape distribution of fisher effort are informed by the ecological theory of functional and numerical responses. Methods and implications of catch-and-release behaviour, multi-species fisheries, and non-catch related fisher site choice are discussed as related to our understanding of fisher behaviour and fisheries outcomes.

Keywords Catch-and-release · Fisher effort · Fishery management · Food webs · Functional response · Ideal free distribution · Landscapes · Numerical response · Predator-prey theory

1 The Discipline of Ecology

Ecology is the scientific study of the processes and interactions that determine the distribution and abundance of organisms (Krebs 2009). Distribution refers to where organisms are found, and abundance refers to how many are found within an area. In ecology, we seek to understand: why this distribution, and why this abundance? Three approaches to answering these questions are descriptive, functional, or evolutionary. Descriptive approaches involve the natural history of organisms across space and time. Functional ecology identifies the processes of interaction among organisms and their interactions with their environment, structured within a cause-and-effect framework. Evolutionary approaches focus on organisms and their interrelationships, considering their evolutionary history. These three approaches provide the core of the science of ecology and are prerequisites to understanding the distribution and abundance of organisms in nature.

Sub-fields of ecology include several levels of integration: individuals, populations, communities, and ecosystems. Ecology of individuals encompasses aspects of behaviour and physiology that shape their interactions and success. Population ecology focusses on demographic processes such as birth, death, immigration, and emigration rates and how these interact in controlling abundance over time and space. Community ecology focusses on interactions among species, such as

competition and predation, and how these processes result in species abundance and composition. And ecosystem ecology focusses on the roles that organisms play in larger global biogeochemical processes within terrestrial, aquatic, and atmospheric systems.

Our approach in this chapter is to examine the behaviour of recreational fishers through an ecological lens based on a combination of field observations, experimentation, simulation models, and theory (Carpenter 1998). Intuitively, recreational fishers and the fish they capture can be viewed as analogous to predator-prey systems. In ecology, our understanding of predator -prey interactions is supported by a richness of empirical and conceptual research on predator-prey interactions, primarily developed within sub-fields of behavioural, population, and community ecology. Ecologically, predator behaviour is presumed to reflect evolutionary selection of behavioural traits that maximize fitness. The ultimate expression of fitness in the natural world is the production of offspring who perpetuate the most successful genotypes. Proximate measures of fitness of the predator are often measured as prey consumption, translating into their growth, survival, and reproductive success. Of course, this analogy is not directly relevant to recreational fisheries where a successful fisher does not necessarily have greater reproductive success! Instead, success is typically measured as high catch rates or the capture of large fish. But, in addition, fishing success (as measured by sociologists and economists as satisfaction and utility; Landon et al. 2026; Melstrom et al. 2026) includes a host of non-catch related characteristics of the fishing experience (e.g. fishers' values for place and culture).

We develop this analogy between predator-prey ecology and fisher behaviour by examining the key underlying processes within a conceptual framework based on simple models. We then characterize several processes that can partially decouple these simple predator-prey interactions, complicating the simple models, and which are likely important within recreational fisheries. The final component of the conceptual framework is the incorporation of predator and prey heterogeneity, that is, several types of fishers and multiple fish species, typical of many recreational fisheries. And finally, we describe the types of data that can inform these ideas and ways in which they are used by ecologists to provide the information needed to understand fisher behaviour and manage recreational fisheries.

1.1 Ecological Predator-Prey Interactions and Fisher Behaviour

Predator-prey interactions can be characterized by two important processes. First is the combination of predator and prey behaviour that results in searching, handling, and consumption of prey by predators, as modified by the avoidance behaviour of prey. In ecology, this aggregate of behaviours results in what is called a "functional response". The second process involves aggregative behaviour of predators across a landscape in response to heterogeneous prey abundance and is termed a "numerical response".

Predator functional responses describe the relationship between prey abundance and the resulting prey consumption rates by predators. Functional responses are determined by predator behaviours such as search time, search efficiency, attack rate, handling time, digestion time, and physiological constraints such as energy content and satiation. In recreational fisheries, functional responses are characterized by the rate of fish capture by an average fisher (expressed as catch-per-unit-effort where effort is in units of time—CPUE) as a function of the abundance of catchable fish. These responses can be proportional, asymptotic, or sigmoid in shape (referred to as Type I, II, or III functional responses) (Fig. 1). In a recreational fishery, the CPUE functional response can be shaped by characteristics like fishing gear selection, use of technology, fisher experience, and fish behaviour (e.g. schools of young fish or adults aggregating on spawning grounds).

Predator numerical responses represent the aggregation (or reproduction) of predators in prey patches with greater abundance or production of prey. Similarly, fishers are expected to choose to participate in fishing or move among fishing sites based on their perception of the quality fishing opportunities available to them. This behaviour leads to a feedback function that characterizes the degree to which fishers as a group are responsive to the assessed quality of the fishing opportunity (i.e. if

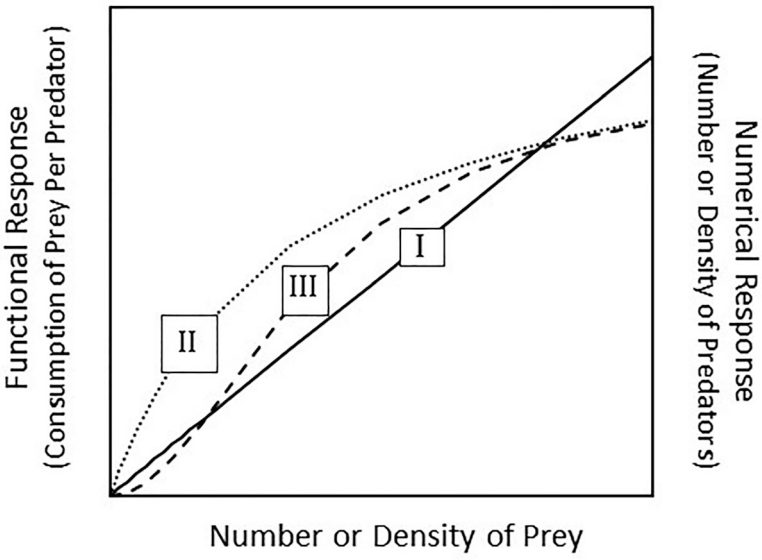

Fig. 1 Functional responses describe the relationship between the number or density of prey and the consumption rate by predators (they can be classified into three types, a linearly increasing consumption rate [Type I], a curvilinear and asymptotic relationship [Type II] and a sigmoid relationship [Type III]), whereas numerical responses describe how the density of predators are distributed across a gradient or prey density (and can be described with the same three types of responses as for functional responses); in recreational fisheries a functional response is measured by catch rates of fish and numerical response by the number of fishers, both as functions of the number or density of fish within targeted fisheries

fishing quality is good, then more effort is attracted, and if poor, then effort is repelled). Therefore, a numerical response is the aggregate outcome of the participation rate and site choice behaviour of a population of fishers.

Predator numerical responses represent behaviours presumed to maximize the fitness of individuals across prey patches when in competition for prey resources with other predators. Under certain ecological assumptions, the spatial pattern that results from these predator behaviours has been characterized conceptually by ecologists as the Ideal Free Distribution theory (Fretwell and Lucas 1969; Gillis et al. 1993). The Ideal Free Distribution concept posits that individual predators will choose prey patches that minimize competition and maximize their fitness (i.e. patches that provide the highest consumption rates). It also assumes that predators have perfect knowledge of the quality of all patches, that predators are ideal—selecting patches that maximize their fitness, and free—implying no costs or constraints on patch choice. Because predators consume prey, increasing predator abundance, and therefore increasing intra-specific competition, will act to disperse predators among patches in such a way that the marginal fitness is equivalent across prey patches. An equal distribution of prey quality across patches will also result in an equal distribution of predator abundances and fitness among patches. But if prey production varies across patches, then predator abundance will be positively related to prey productivity in such a way as to equalize marginal fitness across patches. In recreational fisheries comprised of multiple fishing sites or opportunities (i.e. a set of lakes or streams in a region), the prediction from ideal free distribution theory is that fishers will distribute among these opportunities such that their measures of success become equivalent among all possible fishing sites. The outcome of this fisher behaviour is homogeneity of fisher success across opportunities, but spatial variation in the fisher abundance that is proportional to fish production at individual sites.

In recreational fisheries, the base assumptions underlying the ideal free distribution are often not strictly met, requiring new concepts that better approximate functional and numerical responses. In recreational fisheries, we know there are constraints on getting to and among fishing opportunities based on travel time and costs. Therefore, ideal free distribution "with costs" alters the prediction of homogeneity in satisfaction and fishing quality due to the trade-offs between the benefits of fishing and costs associated with travel. This leads to predictions of "optimal" fisher behaviour where fishers distribute among opportunities in relation to the relative productivity of the various patches, and inversely related to distance as the travel time and costs increase (i.e. fitness in a particular patch is devalued by the costs to acquire the benefits of that patch). In a simple landscape where the productivity of patches is equivalent, the Ideal Free Distribution expectation is a negative exponential decline in the spatial distribution of effort as the distance from the source of the fishers (i.e. population centres) increases across a landscape of fishing opportunities (i.e. fishing lakes).

Application of ideal free distribution theory has provided a simple and robust hypothesis for the behaviour of recreational fishers when faced with a landscape of multiple fishing opportunities (Post et al. 2002; Cox et al. 2003; Parkinson et al. 2004) and provided a deductive engine for modelling studies (Post et al. 2008;

Carruthers et al. 2019; Matsumura et al. 2019). As would be predicted from Ideal Free Distribution, coarse spatial scale field data on fisher catch rates from the British Columbia rainbow trout fishery showed relative homogeneity within regions of similar access costs and inter-regional differences with total fishing effort inversely related to catch rates and positively related to distance from home (Post et al. 2002; Post 2013). This is interpreted as an emergent property of fisher site choice behaviour driven by catch-related fishing quality and access costs (Parkinson et al. 2004). Clearly, fisher site choice is more complex (Hunt 2005; Hunt et al. 2011), but fishing quality and access costs are often among the most important drivers of utility in recreational fisheries (Hunt et al. 2021). In lieu of more detailed descriptions of site-specific attributes, it appears as if catch-related and travel distance-dependent attributes can approximate spatial patterns of effort density and fishing quality at larger spatial scales (Hunt et al. 2011; Wilson et al. 2020) as would be predicted by the ecological foraging processes implied by Ideal Free Distribution theory.

1.2 Predator-Prey Models

Ecologists often build and exercise models designed to ask and answer quantitative questions (Krebs 2009; Hutchings 2021). A modelling approach can increase the rate at which we generate understanding of complex systems. Models are also useful tools to examine dynamic properties of systems based on rates of processes and variability in those rates. Useful models should reflect the true nature of one or more aspects of the system of interest to the researcher. Structurally, a model is a formal expression of the relationship between defined entities of the system in mathematical terms. Predator-prey systems, and fisher behaviour in response to prey characteristics, are complex systems that have been widely studied through the application of models. Functional and numerical responses within predator-prey system models are inherently quantitative and dynamic and provide an effective tool to study their system properties. Here, we develop simple models of predator and prey behaviour and their interactions and examine situations where there are important deviations from simple model representations of recreational fisheries.

At the core of our understanding of fisher behaviour within and among fisheries, measured as aggregate fishing effort, is the dynamic interaction between fishers and their fish resources. Fishing can alter abundance, size structure, behaviour, demographic rates, and species composition of fish communities. These changes to the fish community alter fishing quality as perceived by fishers, which in turn creates feedback among fisher behaviours, site choice, and total fishing effort. Therefore, we need to acknowledge this feedback to understand both fisher behaviours and the fishing outcomes.

To understand feedback between fisher behaviour and fish populations, we again borrow from ecological predator-prey theory and models (Clark 2006, 2018). Fisher harvest is analogous to predators consuming prey and prey (fish) populations are

controlled by ecological production (the aggregate outcome of birth and death processes). In the simplest structure with a fixed fishing effort, we use a Gordon-Schaefer model:

$$\mathrm{d}N/\mathrm{d}t = \text{Production} - \text{Harvest} \tag{1}$$

$$\text{Production} = r \cdot N \cdot (1 - N/K) \tag{2}$$

$$\text{Harvest} = \text{Catch} = C = q \cdot E \cdot N \tag{3}$$

where $\mathrm{d}N/\mathrm{d}t$ is the rate of change in the fish population, which is the difference between the production rate of the population, represented here by logistic population growth, and harvest by fishers. Harvest is the product of the number of fish in the population, N, total fishing effort, E, and the efficiency of that fishing effort, q, if it is assumed that all fish captured are harvested. This simple formulation describes a Type I functional response where the harvest is proportional to fish abundance based on a constant fisher efficiency (analogous to predator attack rate). The efficiency of the fisher-predator (q) is typically referred to as "catchability" in fisheries science and is a fundamental parameter representing the linkage between fishers and fish. Fisher perceptions of fish abundance and fishing quality are based on the number of fish captured compared to the time spent fishing, known as catch per unit effort (CPUE). Rearranging Eq. 3, we see that fisher CPUE (C/E) in this simple formulation is proportional to the fish abundance as $q{\cdot}N$. Therefore, catchability is just as important as fish abundance for determining fishing outcomes. Numerically, q represents the proportion of the fish population that is caught per unit of fisher effort. Many components of fisher and fishery manager behaviours are buried in this seemingly simple term (e.g. choice of gear, knowledge and skill of the fishers, catch regulations, restrictions), plus fish behaviours (e.g. feeding aggressiveness, degree of aggregation). Many of these fish and fisher behaviours can shift q from a constant to a fish density-dependent parameter, which leads to a non-linear functional response (e.g. Type II).

The next step in understanding how fisher behaviour and fishing quality interact is to build into the general model the idea that there is a numerical response to fishing quality. The relationship between CPUE and fish abundance is a key component of predicting harvest rates, and importantly, will guide the numerical (effort) response. Unlike the simple model above (Eq. 3) with a constant E, fisher effort is expected to respond dynamically to changes in fishing quality.

$$E = f(\text{quality}). \tag{4}$$

The CPUE is often a key indicator of fishing quality. Therefore, the relationship between CPUE and $q{\cdot}N$ has an enormous influence on how fisher effort (which drives harvest) responds to fish abundance (as with Type I, II, or III numerical responses in Ecology).

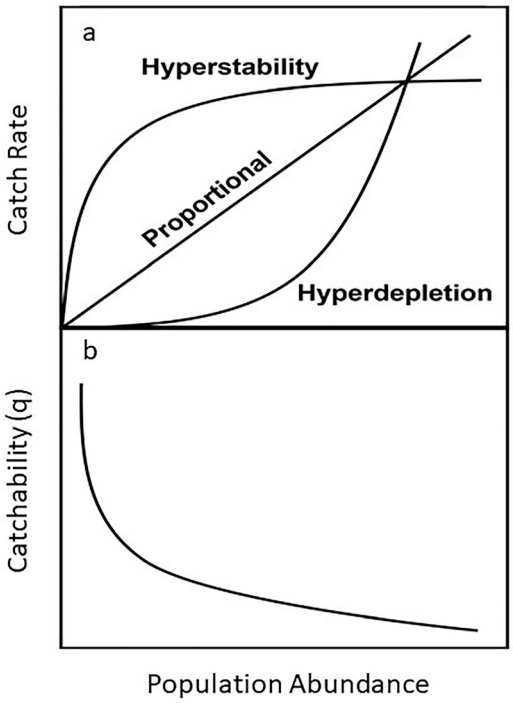

Fig. 2 (**a**) Catch rate (fish caught per time or effort) can be related to population abundance in three ways (many simple models presume that catch rate will increase proportionately with abundance fish in the population presuming random encounter of homogeneous fishers and fish, but other mechanisms can lead to either an asymptotically increasing or exponentially increasing catch with increasing fish abundance; these alternate mechanisms can lead to either hyperstability or hyperdepletion of catch rates as populations decline in response to harvest) (**b**) hyperstable catch rates imply that catchability (q) is low at high fish population abundance and increases as fish abundance declines (which has the effect of accelerating rates of harvest as fish populations decline due to harvest)

Traditional fisheries management tenets have often assumed that the relationship between fisher CPUE and fish population size is proportional, like the Type I functional response in ecological predator-prey interactions (Figs. 1 and 2). This assumes that fishers will leave a waterbody when catch rates become unsatisfactory and seek alternative, higher catch rate opportunities, consistent with predictions from the ideal free distribution theory. Self-regulating fisher behaviour could potentially lead to a sustainable equilibrium if fishers become dissatisfied and leave before the fishery becomes overharvested (Askey and Johnston 2013). However, non-linear functional responses lead to hyperstability or hyperdepletion and therefore can impede a self-regulating equilibrium.

1.3 Departures from Simple Predator-Prey Models

In its simplest formulation, predator-prey theory postulates that the local abundance of predators and their consumption are tightly linked to the abundance of local prey. In this case, if catch rates decline, then fisher effort will decline proportionately as fishers leave the system (Fig. 2a). However, there are many factors that may cause a partial disconnect between predator and prey populations, particularly in recreational fisheries. Such disconnects can have deleterious results for the prey population.

If fish aggregate, either in schools or in association with habitat types, and if fishers can find these aggregations, then catch rates can remain high despite reductions in density due to harvest (Post et al. 2002). Likewise, catch rates may saturate at higher fish densities due to fisher handling time (e.g. hooking, playing, harvesting, or releasing a fish) similar to a Type II functional response between predator consumption and prey density (Fig. 1). This density-dependent catchability, where q increases as populations decline, leads to an undesirable and pathological result in which CPUE is hyperstable, declining little with declining fish populations (Fig. 2b). If this is the case, then there is little or no signal to fishers that the fish population is declining, and therefore no resulting fisher numerical response to abandon a declining fish population. This depensatory process is an important outcome of the interaction between fish and fisher behaviours, and one that can lead to overfishing and collapse (Post et al. 2002; Sass et al. 2021). The opposite outcome, in which fishing in relatively pristine conditions selectively removes the most spatially or behaviourally vulnerable fish, resulting in a rapid decline in catch rate, is termed hyperdepletion (Fig. 2a). Such fisheries would likely lead to reduced effort as CPUE would not be attractive (Biro and Post 2008).

An early exploration of functional responses in recreational fisheries was for a Wisconsin walleye (*Sander vitreus*) fishery, where a linearly increasing (Type I) relationship between catch rate and fish abundance was identified (Johnson and Carpenter 1994). Yet, other analyses identified curvilinear relationships for both Ontario (Shuter et al. 1998; Post et al. 2002) and Yukon Territory lake trout (*Salvelinus namaycush*) (Wilson et al. 2020) and California marine bass (*Paralabrax* spp.) (Erisman et al. 2011). Hyperdepletion has been observed in recreational fisheries where, after an initial period of high catch rates of the most vulnerable fish in a population, CPUE stabilizes with reductions in stock size due to harvest, fish learning behaviour, and refractory (invulnerable) periods following capture and release (Cox and Walters 2002; Askey et al. 2006; Cline et al. 2012; Sass et al. 2018; Alós et al. 2019). In contrast, recreational fishers and fish behaviour can also lead to hyperstability through several mechanisms: effort sorting (i.e. more skilled fishers maintaining high catch rates as stock size declines), use of technology, fish spawning aggregations, and selective habitat use by fish (Hansen et al. 2005; Ward et al. 2013; van Poorten et al. 2016; Mrnak et al. 2018; Dassow et al. 2020; Feiner et al. 2020). Observed strengths of hyperstability and hyperdepletion patterns vary among geographic locations and among species in recreational fisheries (Mogensen et al. 2014; Mosley et al. 2022), and it needs to be recognized in these situations that catch rates provide biased measures of population status.

The behaviour of recreational fishers is not always driven by harvest, but instead by catch. Catch can include harvested and released fish. Moreover, the numerical response of fishers to catch can be weak if the primary site choice characteristics are not based on fish abundance. For example, fishing sites that are close to fishers, sites with improved access and facilities (paved roads, restrooms, boat ramps, lodging, or campsites), and aesthetics (e.g. pristine lake shorelines, water quality) can all influence fisher effort relatively independently of fish abundance. These factors can decouple the predator-prey dynamic as represented in Eq. 3, but in separate ways and with contrasting outcomes. Catch-and-release is interpreted by some as an absence of fishing mortality (although some level of discard mortality inevitably occurs) and would therefore eliminate the fisher numerical response presumed earlier to be driven by depletion. Revisiting the Gordon-Schaefer model:

$$\text{Harvest} = q \cdot E \cdot N \cdot (\alpha + \beta) \tag{5}$$

α is the proportion of the catch that is retained (i.e. harvested) and β is the proportion of released fish that die from capture, handling, and release. Both α and β are features of fisher behaviour—related to individual or legislated decisions to release fish and individual skills to effectively capture, handle, and release fish to minimize subsequent mortality. The other key component impacting harvest is fishing effort, E. If the proportion of the catch retained (α) and release mortality (β) are zero, then the impact of fishing on fish populations is benign. However, if effort is sufficiently high and harvest exceeds production, then overfishing can result.

Furthermore, fisher behaviour may not be driven by either harvest or catch, but instead by a variety of non-catch related attributes (Lewin et al. 2006). The influence of non-catch related attributes on where fishers fish can result in a disconnect within the predator-prey system. This can lead to fisher behaviour that is not tightly tied to fish abundance and therefore no longer self-regulating. Numerically, fishing effort is neither constant as depicted in Eq. 3 nor related to fishing quality (i.e. CPUE) as in Eq. 4. These departures from a strong linkage between predator and prey can have significant impacts on fisheries. For example, fisheries that are close to urban centres may maintain elevated levels of fishing pressure despite low fishing quality; in these instances, fishing pressure could be sufficient to collapse fish populations (Post et al. 2002, 2008; Hunt et al. 2011). Regulations and stocking practices may also influence where fishers choose to fish, potentially leading to exploitation rates that are not correlated with fish abundance (e.g. Beard et al. 2003; Johnston et al. 2007; Mee et al. 2016).

1.4 Multiple Predator "Species"

Now, let us move away from a single predator-prey system. Imagine a system where the prey population is targeted by multiple predator types. This implies that a single functional or numerical response will be inappropriate in characterizing predator and

prey behaviours. There is widespread evidence in recreational fisheries supporting heterogeneity of fisher behaviours (Beardmore et al. 2013; Dabrowska et al. 2017). Therefore, an approach adopted by ecologists is to assess evidence for clusters of traits and behaviours of fishers and segmentation into different "species" or types of fishers. Traits often considered in this segmentation include the importance of catch rate, fish size (e.g. trophy fish), harvest tendency, fishing frequency (avidity), willingness to travel (costs), and skill (q). Pioneering work on specialization identified four to seven distinct groups of fishers that differentiate along a specialization continuum (Bryan 1977; Fisher 1997). More recent studies of fisher heterogeneity have found that three to four groups often adequately describe the variance and association among traits and behaviours of recreational fishers (e.g. Oh et al. 2005; Oh and Ditton 2006; Dorow et al. 2010; Beardmore et al. 2013; Ward et al. 2013). For example, some fishers may be more consumptively oriented and particularly interested in harvest, whereas others may be more trophy-oriented and place more emphasis on the size of fish caught rather than the number of fish caught (Johnston et al. 2010; Hunt et al. 2021). Furthermore, individual fisher's preferences may not be consistent temporally or among species. Harvest orientation may also decline over time or with age as fishers become more specialized (Bryan 1977, but see Dorow et al. 2010; Embke et al. 2020; Hunt et al. 2021). The impact on the fish resource of multiple fisher segments, and their relative abundance within a fishery, can differ due to differences in annual fishing effort, catchability, and thus catch rates, and propensity to harvest fish (e.g. Ward et al. 2013). Simulation models can be useful to assess the impacts of this heterogeneity in fisher behaviour within fisheries (e.g. Johnston et al. 2010; van Poorten and Camp 2019) where the ecological analogy is multiple predator species competing and behaving differentially in the predator-prey interaction.

Understanding the source of behavioural variability among fishers is crucial to effectively manage recreational fisheries. Recognizing that fishers do not behave homogeneously in response to catch, in willingness to travel and accepting additional costs, or in efficiency and skill level, indicates that a single functional or numerical response relationship is an inappropriate description of fisher behaviour (van Poorten and Camp 2019). However, functional and numerical responses of an entire population of fishers are simply phenomenological descriptions of behavioural traits of many individual fishers. In other words, there is a richness of individual behaviours that, in aggregate, result in fishery-wide patterns. Despite these limitations, simple phenomenological descriptors of population-level processes have been useful in understanding patterns seen in real-world fisheries (Post et al. 2002; Askey et al. 2013).

1.5 Multiple Prey Populations

In addition to multiple types of predators, there is also often heterogeneity in key attributes of fish resources distributed across landscapes (e.g. production, abundance, and size-structure, fisher demand, distance from fishers' homes, and a host

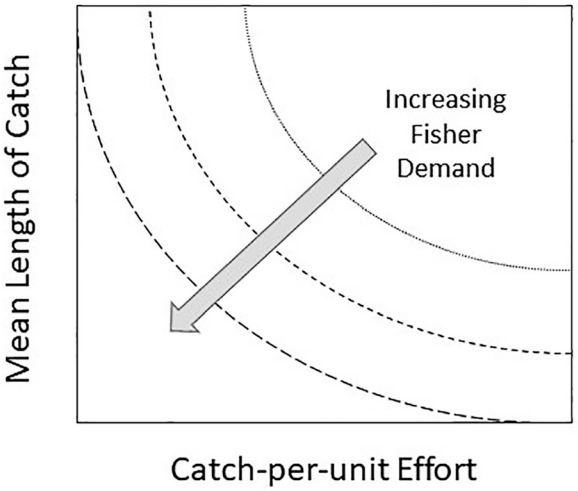

Fig. 3 Size-number trade-offs where the combination of density-dependent fish ecology and fisher behaviour constrain the combination of fish density, fishing catch per unit effort, and mean length of the catch (increasing fisher demand reduces the trade-offs between realized catch-per-unit effort and mean length of catch)

of other site-specific characteristics) (Cantin et al. 2021). Although fishers would likely prefer fisheries with high catch rates of large fish, density-dependent ecological processes typically result in fish populations with either high density of small fish or low density of large fish (Post and Parkinson 2012; Persson et al. 2014). The equilibrium outcome of the combination of these ecological trade-offs and heterogeneity among fisher preference in catch rate and fish size is an equal fishing quality isopleth within fisheries sharing other non-fish traits (Parkinson et al. 2004; Wilson et al. 2016) (Fig. 3). The greater the fisher demand, driven by non-catch related fishery traits such as travel time or distance, the closer the quality isopleth is to the axes with reduced catch rate and reduced fish size (Fig. 3). This outcome is an emergent property of heterogeneity of fisher behaviours and ecological processes distributed across landscapes of recreational fisheries.

Feedbacks between fisher behaviour and fish population characteristics create a dynamic where fisher behaviour is responsive to both local and landscape conditions and is therefore context specific. Even so, most empirical studies of fisher behaviour reveal only behavioural responses to the local conditions. Understanding processes that drive decision making in fisher behaviour is best explored with experimental manipulation of key drivers with controls (as developed in van Putten et al. 2026). Such experimental data are scarce, so models of site choice behaviour by multiple types of fishers can be simulated across complex landscapes of travel distances, fish abundances, and other site characteristics to predict equilibrium landscape patterns in the aggregate of fisher behaviour and fishery outcomes (Carruthers et al. 2019; Matsumura et al. 2019).

A further consideration is that although some recreational fisheries have a single species focus, others are multi-species. Fishers may target a focal species through their choice of gear and fishing locations, but influence more than one species (or sub-population) because of their fishing tactics. Now we see that a recreational fishery can have multiple fisher types that are fishing over multiple single or multi-

species fishing sites that can vary in travel time and access costs across a diverse landscape. Further, recreational fishers are often influenced by regulations, where closed seasons or restrictive harvest limits can cause fisher behaviour to target alternate species in alternate places (Chagaris et al. 2019) or co-occurring species with more liberal regulations (e.g. open seasons, length limits; Murphy et al. 2019). Density-dependent prey switching behaviour by fishers may alter a fishery if fishers attempt to maximize their catch independent of species. Catchability also varies among species; thus, it may be that regardless of fisher stated preference, lower preference but higher q species will have higher catch rates and can lead to overharvest. Although not all recreational fisheries are this complex, these sources of variability in fisher behaviour highlight the diverse axes over which fisher behaviour can be expressed. Differential species preferences and harvest regulations interact with fisher behaviour types to modify site, gear, and harvest choices, which can have deleterious consequences for some fish populations (Johnston et al. 2013). The ecological approach to understanding fisher behaviours and resulting fishery dynamics in systems with multiple fisher types, multiple fish species, and management attempts to manipulate fishery outcomes can be characterized using multi-factorial predator-prey behavioural relationships, but these social-ecological systems are often complex (Ward et al. 2016). These systems are often best assessed through simulation of integrated social-ecological models (Carruthers et al. 2019; Matsumura et al. 2019; and see Jensen et al. 2026) and empirically using adaptive and experimental management experiments (van Putten et al. 2026).

An additional challenge in multi-species fisheries is the presence of a less preferred, but abundant, alternate species which might provide sufficient attraction to a fishery to maintain fisher effort on a waterbody despite a depleted preferred species, leading to concerns of collapse of the preferred species (Marshall and MacCrimmon 1970; Nguyen et al. 2012; Chagaris et al. 2019). But these observations are not universal—imposition of restrictive regulations can also repel effort, as was observed after implementing catch and release in a former harvest-oriented fishery for bull trout (*Salvelinus confluentus*) in Alberta (Johnston et al. 2007). This decoupling of fisher numerical response behaviour and regulations necessitates ecosystem-based fisheries management and explicit consideration of fisher behaviour as integral to these dynamic social-ecological systems (see van Putten et al. 2026; Jensen et al. 2026).

1.6 Abiotic Habitat Considerations

Not all decisions on where and when predators feed are related to prey availability. Predators also make behavioural decisions based on abiotic factors, such as habitat preferences, temperature, and competition with other predators. These variables may not be the primary motivation leading a predator to one site over another but play a role in their decision. Fishers also make choices on where and when to fish based on factors beyond the species, size, and number of fish they may catch. These are referred to as non-catch related attributes of fisher decision-making.

Both catch and non-catch related attributes are determinants of fisher satisfaction (Birdsong et al. 2021). Catch-related fishing quality includes attributes such as species, catch rate and harvest rate, and size of fish caught. Spatial behaviour is influenced by costs to access fish resources (e.g. travel distance, road access quality, licence fees, gear costs). Hunt (2005) and Hunt et al. (2019) have suggested five non-catch related attributes that, in addition to travel cost, play a significant role in fishers' motivations to choose a site: environmental quality, facility quality, regulations, congestion, and destination size. Other non-catch attributes include amenities (e.g. campgrounds, toilets, boat launch), lake characteristics (e.g. destination size, environmental quality), regulations and management (e.g. length restrictions, daily bag limits, gear and motor restrictions, stocking policies; Dabrowska et al. 2017). Each fisher will weigh the expected benefits of fishing a system (e.g. high catch rate, large fish, location on the landscape) with conditions that may be less favourable, resulting in implicit trade-offs among attributes. For example, fishers may choose to fish a system with a boat launch that has lower catch rates and smaller fish that is close to home, rather than a system with hike-in only access with higher catch rates and larger fish, that is farther away, and less crowded. Non-catch related attributes tend to be more stable over time (e.g. regulations change slowly, amenities are not regularly upgraded, and lake size and location do not change) than do catch-related attributes. Thus, non-catch attributes may be hard for managers to influence. However, satisfaction from non-catch related motives for going fishing, such as relaxation, getting out in nature, and socialization, may be more easily achieved or at least controlled by fishers when they choose a site (Arlinghaus et al. 2017; Beardmore et al. 2015), regardless of the fishing quality. In contrast, catch-related attributes are where most management actions are targeted, but they may be harder to predict, and catch-related motives for fishing (e.g. to catch lots of big fish) are often harder to satisfy. Thus, catch-related attributes may ultimately have a greater influence on fisher satisfaction and future fishing decisions (Arlinghaus et al. 2017; Beardmore et al. 2015; Birdsong et al. 2021).

Although the ecological approaches of functional and numerical responses and Ideal Free Distribution (dependent on catch-related attributes) have been useful in understanding fisheries dynamics, it is clear that non-catch-related attributes can also be important drivers of fisher behaviour. As the importance of non-catch-related attributes grows, the disconnect between the numerical response of the fisher to the fish prey increases, leading to a move away from a typical Type I response. For example, if distance is critical for fishers in determining where they fish, fisheries close to larger population centres will experience greater fishing pressure even when catch rates are reduced simply due to proximity. Some fish populations may not be able to support such pressure and could collapse. At a minimum, the increased pressure will lead to changes in fishing quality and the isopleth describing the trade-off between fish size and catch (Fig. 3). The importance on non-catch-related attributes in driving fisher behaviour is the reason that approaches that integrate socio-ecological dynamics are necessary to fully characterize the complex feedbacks within and dynamics of recreational fisheries.

1.7 Non-lethal Impacts

A key attribute of fisher behaviour is their propensity to harvest their catch—traditionally, harvest was a primary motivation for fishing. This behaviour aligned fishers, as predators, well with ecological predator-prey models. Although many recreational fishers remain harvest-oriented (Gaeta et al. 2013; Chagaris et al. 2019; Embke et al. 2020), social norms of nearly exclusive catch-and-release have emerged for some fish species, particularly in North America (e.g. black bass *Micropterus* spp., muskellunge *Esox masquinongy,* trout *Oncorhynchus* spp., and *Salvelinus* spp.) (Sass and Shaw 2020). Predominantly catch-and-release fisheries decouple fishers as predators in ecological models, especially in situations where the product of release mortality and fishing effort is low (i.e. β and E in Eq. 5) and compliance with mandatory release is high (Sullivan 2002; Post et al. 2003). Regulation-mandated fisher behaviour requiring release generally derives from one of two management goals. First is a conservation goal designed to ensure that overfishing neither compromises the sustainability of the targeted populations nor the social and economic values of the recreational fishery (Allen et al. 2008; Rypel et al. 2016). Second is a social goal designed to maintain or enhance trophy fish potential despite enhanced fishing effort (e.g. complete catch-and-release, restrictive minimum length limits, low bag limits). Voluntary release, on the other hand, is a fisher's personal behavioural choice often in support of a conservation ethos (Sass and Shaw 2020). Counter to a catch-and-release approach is a growing ethical argument against release behaviour grounded in animal welfare concerns. This is particularly predominant in some Western European countries and Indigenous cultures in North America (Arlinghaus et al. 2007, 2012).

The regulation of fisher behaviour via partial catch-and-release (e.g. length limits, bag limits) or complete catch-and-release is often used to attempt to structure fish populations to meet fisher and management goals for fishing quality. Although catch-and-release fishing has been promoted for fish conservation (and has been successful, and maybe overly successful in some cases) (Allen et al. 2008; Rypel et al. 2016), the practice can also result in species-specific over abundances, shifts in fish community composition, and regulation ineffectiveness to structure fish populations (Sinnatamby et al. 2023). Satisfying goals for catch rate and size structure (functional responses), and the provision of fishing opportunities (numerical responses) across gradients of fish abundance can be used to characterize the performance of fisheries. Liberal harvest regulations may result in reduced catch rates, higher individual fish growth rates, and greater trophy fish potential. In contrast, conservative regulations often result in the opposite results in fish populations. Therefore, managers are tasked with implementing harvest regulations that attempt to control fisher behaviour to achieve a balance among these three key ecological measures—catch rates, growth rates, and trophy-fish abundance. As such, predominant voluntary release can lead to regulation ineffectiveness in structuring fish populations. For example, a 28-year program of length-based harvest regulations on a Mississippi reservoir failed to restructure the largemouth bass population

due to predominant voluntary release (α in Eq. 5) (Hessenauer et al. 2018; Miranda et al. 2017). Voluntary release, in the absence of discard mortality and sublethal effects, eliminates the role that fisher behaviour plays in structuring fish populations. Therefore, fisheries management must consider fisher behaviour where high release rates have the potential to decouple harvest from regulation effectiveness in structuring fish populations.

2 Measuring Fisher Behaviour and Fishery Outcomes

Assessing fisher behaviour, and fish population and community outcomes in recreational fisheries requires data on both fisher and fish. Key variables for assessing fisher behaviour include estimates of fisher effort (i.e. fish species-specific and total effort) and species-specific catch, harvest, and release rates. Data on the size of fish caught, catch and harvest rates, fishing effort, and species information are often collected using intercept surveys (roving or access point surveys) of fishers at a waterbody, often called creel surveys (Pollock et al. 1994; de Kerckhove et al. 2026). Species-specific release rates are critical for assessing fisher behaviour in fisheries managed for multiple species but have often been excluded from traditional creel surveys (but see Sass et al. 2022a). These surveys and their data provide an understanding of the impact of fishers on the fish populations (e.g. catch and harvest), their revealed preference in the conditions offered at that place and time (e.g. fishing effort), as well as an opportunity to informally talk with fishers about what attracted them to the fishery, things they dislike about the fishery and broader questions about regulations and fishery management. Methods for conducting these surveys and analysing the data to provide estimates of fisher effort, catch, and harvest aggregated over a season are available in many sources (e.g. Pollock et al. 1994; Jones and Pollock 2013). Fisher diary surveys (e.g. Gaeta et al. 2013), and mail or phone, or email surveys (e.g. Gundelund et al. 2020) have also been used to estimate effort, catch, harvest, and release rates. Stated preference surveys have also been used to predict fisher behaviour where fishers are offered a diversity of hypothetical site characteristics among which to choose (e.g. Beardmore et al. 2015; Dabrowska et al. 2017).

Technology is increasingly playing a role in supplementing information on fishers and their impact on fisheries. Citizen science projects and the expansion of digital platforms such as online forums or mobile phone apps are increasingly being used in fisheries data collection (e.g. Jiorle et al. 2016; Gundelund et al. 2020; Johnston et al. 2022; Venturelli et al. 2026). Traditionally, fisher effort has been estimated through creel surveys, although technology (e.g. car counters, drones, parking lot counts, satellite imagery, trail cameras, aerial flights, video surveillance) has improved our predictions of fisher effort dynamics over time (e.g. van Poorten et al. 2015; Hartill et al. 2016; van Poorten and Brydle 2018; Dutterer et al. 2020). Importantly, several of these high-frequency automated methods improve the precision of fishing effort estimates, thereby improving the ability of managers to detect

fishing responses to changes in fishing conditions or regulations. New analytical techniques are also being developed that help borrow information across fishing sites, allowing for landscape patterns in fishing effort to be estimated (Trudeau et al. 2021). These technological advances hold great promise for quantifying fisher effort dynamics across fishing sites, and potentially across multi-species fisheries. For example, quantifying changes in fishing effort in response to changes in length limits and seasonal closures is a key need, and automated surveys can save substantial time and effort. Including fisher primary and secondary residence zip code information in creel surveys has proved invaluable for monitoring fisher effort across fisheries landscapes (Kaemingk et al. 2021; Lant et al. 2022). To monitor outcomes in fisheries managed for multiple species, common fisheries-independent surveys are used to estimate species-specific abundances (e.g. mark-recapture population estimates) or relative abundances (e.g. catch-per-unit-effort) and fish demographics (e.g. length, weight, age).

2.1 Functional Responses: Catchability and Catch-Per-Unit Effort

Functional responses in the context of recreational fisheries link a key metric, mean catch rate (in units of catch per unit effort; CPUE), to the availability of catchable fish (usually measured in units of abundance or density) (Johnson and Carpenter 1994). Catch rate is a key measure of success and satisfaction in recreational fisheries and is estimated from creel surveys of fishers, either as they complete their fishing trip or when they are in the process of fishing.

Establishing a functional response for a fishery is a data-intensive endeavour that requires experimental or empirical contrasts in fish densities and fishery-independent measures of abundance. For many fish species, estimating the total fish population size can be exceedingly difficult, and, in those cases, catchability can be estimated using intensive mark and recapture programs. In these programs, large numbers of fish are marked using a tag or other identifiable mark, and the number of harvested fish with a mark provides an estimate of the fishing mortality rate. Catchability is then estimated as the fishing mortality rate divided by the fishing effort that generated it. Given the substantial data requirements, functional responses and associated density-dependent catchability estimates are not often measured and reported in the literature.

2.2 Numerical Responses: Fisher Effort Across Landscapes

Fisher behaviour, through site choice, is often referred to as an effort response at the population level—equivalent to numerical response in ecological terms (Post 2013). An effort response is the result of the aggregate decision-making by a population of

fishers to the quality of the fishery—where quality is measured by fish abundances or catch rates. Because fishing quality is often one of the primary determinants of site choice, effort is attracted by high and repelled by low fishing quality (Post et al. 2008; Post and Parkinson 2012). The numerical effort response behaviour by fishers on individual fisheries is typically measured through creel surveys designed to estimate total effort on a water body in relation to the abundance of catchable fish. This approach has been used in fisheries like Pacific salmon (*Oncorhynchus* spp.) and kokanee (*O. nerka*) troll fisheries in British Columbia (Cox et al. 2002; Askey 2016) and in an Ontario lake trout fishery (Shuter et al. 1998; Post et al. 2002). In other cases, these relationships are established by collecting data over many individual fishers within a lake district, as in Wisconsin walleye (Johnson and Carpenter 1994), British Columbia rainbow trout (*O. mykiss*) (Post et al. 2008; Carruthers et al. 2019; Cantin et al. 2021), and Yukon Territory lake trout fisheries (Wilson et al. 2020). In contrast, Camp et al. (2016) evaluated fishing effort and fish abundance in multiple marine fisheries and documented little evidence of a numerical response, suggesting multiple social factors may overwhelm the traditional link between these two variables.

In contrast to these empirical observations of effort and fish abundance across landscapes that are used to reveal a pattern, other studies use stated choice surveys to predict the probability of fishing given catch rates (Beardmore et al. 2015; Dabrowska et al. 2017). A review of shapes of effort response curves for multiple species and ecological groupings of recreational fisheries revealed Type I, II, and III numerical responses using this alternate approach (Golden et al. 2022). The functional responses differed among fisheries in both the range of effort and the responsiveness of effort to fish catch rates (Golden et al. 2022).

An important means of understanding numerical responses is through simulation models that take insights, theories, and methods described above to make predictions on how diverse fishers will distribute across the landscape and interact with fish populations. Latent class models, principal component analyses, or hierarchical cluster analyses are some of the methods used to test for the presence of groups of fisher types within datasets of fisher behaviours (Fisher 1997; Dorow et al. 2010; Beardmore et al. 2013; Ward et al. 2013; also see Melstrom et al. 2026; Mackay et al. 2026). Data for these types of analyses may come from choice experiments that state intended behaviour (e.g. Beardmore et al. 2013), or from sources such as creel surveys, mail and web surveys, and fisher diaries that reveal actual behaviour (e.g. Ward et al. 2013). Social-ecological modelling frameworks integrate feedback among fishers, managers, and fish populations to explore the impacts of various management scenarios (e.g. Johnston et al. 2018; Matsumura et al. 2019; Carruthers et al. 2019; Wilson et al. 2020). Understanding the diversity of fisher behaviour is useful in contrasting the effectiveness of regulations designed to sustain fisheries. Given the diversity of fishers in populations, studies suggest that managers should seek to provide a variety of fishing opportunities that appeal to heterogeneous fisher populations, rather than using one-size-fits-all policies (Ward et al. 2013; van Poorten and Camp 2019). These insights could not have been gained without careful integration of multiple lines of evidence through models.

2.3 Catch-and-Release Fishing Behaviour

Estimating species-specific release rates generally requires the collection of catch-and-release information during creel surveys or in fisher diary surveys (Gaeta et al. 2013; Gilbert and Sass 2016; Shaw et al. 2019; Sass et al. 2022b). Unfortunately, traditional creel surveys often only record information from harvested fish, not released fish. To estimate release rates, creel surveys and fisher diary surveys should be designed to specifically capture this aspect of recreational fisheries and be coupled with fisheries-independent surveys to assess population responses (Sass et al. 2022a, b). This can be accomplished by estimating and modelling the components of the Gordon-Schaefer model with additional components to incorporate fisher release mortality (as in Eqs. 1, 2, 3, 4, and 5), derived from ecological predator-prey theory. Understanding the dynamics of fisher behaviour in catch-and-release fisheries is crucial in managing these recreational fisheries.

2.4 Fisher Behaviour in Multi-species Fisheries

Although the methods of assessing fisher behaviour in multi-species fisheries do not differ from single-species fisheries, fisher behaviour in these multi-species systems can result in complex and often undesirable fishery outcomes. In fisheries where some species are predominantly released voluntarily and others are harvested, density-dependent effects on growth and alterations to the food web can occur. High voluntary release rates of largemouth bass (*Micropterus salmoides*) and muskellunge (*Esox masquinongy*) have resulted in reduced individual growth rates and a decrease in the catch of large fish (Hansen et al. 2015; Gilbert and Sass 2016; Shaw et al. 2019; Sass and Shaw 2020). High largemouth bass abundances and a lack of bullhead *Ameiurus* spp. harvest has also negatively influenced walleye recruitment (Hansen et al. 2018; Sikora et al. 2021). Even following fisheries closure for the harvested species, the alteration of food web structure in these situations can remain persistent and cause the fishery to collapse or stock recovery to be delayed (Walters and Kitchell 2001; Post et al. 2002; but see Cahill et al. 2022). In some multispecies Salmonid fisheries, fishers have been incentivized with rewards to encourage targeting and to discourage voluntary release of predatory rainbow trout and lake trout to recover a collapsed prey species, kokanee, which is also a popular fishery (Hansen et al. 2010; Warnock et al. 2022). These shifts in fish species composition favouring one species over another due to voluntary release have the potential to disrupt the balance between catch rates and trophy fish potential, not meet diverse fisher desires, lead to single-species regulation ineffectiveness, and highlight the need for ecosystem-based fisheries management and the recognition of recreational fisheries as social-ecological systems (Solomon et al. 2020).

2.5 Non-catch-Related Fisher Site Choice

Fisher preferences for various attributes of a fishery are often determined from revealed preference models (actual behaviour) or stated preference models (intended behaviour) (Hunt et al. 2019). These two approaches are disciplinarily rooted. The ecological approach of assessing numerical response of fishers to temporal and spatial variation in fishing quality typically involves observations of fishing effort, analogous to assessments of predator abundance in relation to prey abundance distribution (i.e. the revealed preference of the predators). Whereas stated preference models derive from projections of future behaviour, from statements of preference or intent, as developed in survey design in the social sciences. Linear and additive relationships describing the effects of various attributes of fisher utility (i.e. satisfaction, benefit) are generally assumed, but these assumptions are often not assessed (Hunt et al. 2019). Non-linearities in the relationships between realized utility (i.e. satisfaction, benefit) and the various attributes could alter the relative influence of different attributes on fishing decisions (Johnston et al. 2010; Hunt et al. 2019). For example, the change in utility from catching zero fish versus one fish may not be the same as the difference in utility between catching one fish versus two fish, or ten fish versus eleven fish. One might expect a diminishing benefit as catch rates increase (Johnston et al. 2010; Arlinghaus et al. 2014). For example, Patterson and Sullivan (2013) found that fishing effort on put-and-take rainbow trout fisheries in Alberta was strongly related to the distance from population centres but not to catch rates, and that satisfaction was logarithmically related to catch rates. Thus, catch rates may be an important predictor for fisher site choices when they are low, whereas other attributes may become critical in determining fishers' fishing decisions when catch rates are moderate or high.

3 Future Research

Our review of the ecological science perspectives and approaches to understanding fisher behaviour and the dynamic outcomes of their interaction with fishes has identified a number of gaps in understanding, providing a useful research agenda. These gaps can be characterized as a need for (1) enhanced understanding of processes, (2) understanding methodological biases and technological innovation, and (3) enhanced integration across the fields and methods of social, ecological, and data sciences.

Temporal trends in social and ecological processes have the potential to mischaracterize recreational fisheries if viewed as status quo or static. For example, trends away from a consumptive paradigm towards increasing conservation approaches have been observed broadly, but there is substantial variation among

recreational fisheries in this trend. In addition, increasing concerns for animal welfare involving regulations preventing catch-and-release are growing, particularly within some jurisdictions (Arlinghaus et al. 2012). Temporal trends in demography involving deficits in recruitment of young fishers and aging of populations can shift fishing effort, species preferences, and site selection by fishers. And in the longer term, it is possible that changes in the proportion of people who live in cities, and changes in fishers' travel habits, as concerns about the climate impact of travel increase, may lead to broad-scale changes in how fishers distribute over the landscape. And lastly, climate change and its impact on aquatic ecosystems will likely alter production and species composition of recreational fishes and modify feedback to angler behaviour through functional and numerical responses. Spatial heterogeneity in the rates and directions of these trends will challenge our understanding of fisher behaviour, fishery outcomes, and assessment of sustainable recreational fisheries.

The predator-prey analogy applied to recreational fishers has been useful in identifying dynamic processes leading to either self-sustaining or overexploited fisheries. The complexity of fisher behaviour, when coupled to fish population and community dynamics, characterized by functional and numerical responses, is useful in identifying management challenges. For example, what are the characteristics of fisher and fish behaviour that result in pathological nonlinearities and risk of overharvest and collapse?

Methodological issues can lead to bias in data and functions derived from creel and stated preference surveys. Although not necessarily without bias, technological innovations in data collection, such as cameras, drones, fishing apps, and GPS trackers, can be used to collect copious amounts of data over substantial temporal and spatial scales that would be extremely expensive using more common methods. Rigorous ground truthing, bias assessment, and correction are important to characterize fisher behaviour for use in dynamic models. These assessments are lacking today.

Though the field of ecology and ecologists may have done much of the heavy lifting early in our exploration of fisher behaviour in recreational fisheries (Johnson and Carpenter 1994; Shuter et al. 1998; Post et al. 2002, 2008; Cox and Walters 2002; Beard et al. 2003; Cox et al. 2003; Parkinson et al. 2004; Askey et al. 2006), the future must involve the development and testing of process-oriented social-ecological systems models. Model validation must effectively integrate temporal and spatial data from fisheries stock assessments and fisher creel and stated preference surveys. Such an approach would provide the tools necessary to more fully understand the role that fisher behaviour plays in fishery outcomes and develop rigorous management strategy evaluations. It would also provide the predictive capacity for the development of adaptive management and structured decision approaches for reducing uncertainty and refining policy decisions—all with the end goal of optimizing recreational fisheries and sustaining their substantial ecological services for fishers and for society.

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