

Ecological surprise: concept, synthesis, and social dimensions

KAREN FILBEE-DEXTER,^{1,2,†} JEREMY PITTMAN,³ HEATHER A. HAIG,⁴ STEVEN M. ALEXANDER,^{5,6}
CELIA C. SYMONS,⁷ AND MATTHEW J. BURKE⁸

¹Marine Section, Norwegian Institute for Water Research, Gaustadalléen 21, Oslo 0349 Norway

²Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia B3H 4R2 Canada

³School of Planning, University of Waterloo, 200 University Avenue West, Waterloo, Ontario N2L 3G1 Canada

⁴Department of Biology, Limnology Laboratory, University of Regina, 3737 Wascana Parkway, Regina, Saskatchewan S4S 0A2 Canada

⁵National Socio-Environmental Synthesis Center, University of Maryland, 1 Park Place, Annapolis, Maryland 21401 USA

⁶Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, Stockholm, 10691 Sweden

⁷Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, 1156 High St., Santa Cruz, California 95064 USA

⁸Department of Natural Resource Sciences and McGill School of Environment, McGill University, 3534 University St., Montréal, Quebec H3A 2A7 Canada

Citation: Filbee-Dexter, K., J. Pittman, H. A. Haig, S. M. Alexander, C. C. Symons, and M. J. Burke. 2017. Ecological surprise: concept, synthesis, and social dimensions. *Ecosphere* 8(12):e02005. 10.1002/ecs2.2005

Abstract. As the extent and intensity of human impacts on ecosystems increase and the capacity of ecosystems to absorb these impacts dwindles, unanticipated behavior in ecological systems—or surprises—is likely to become more common. The concept of ecological surprise is broadly applied but seldom explicitly developed in ecological literature, and ecologists can employ diverging language, frameworks, and interpretations of surprise. Here, we synthesize what ecological surprise has meant to ecologists studying these events and review the development and use of the concept in ecology. We define ecological surprise as a situation where human expectations or predictions of natural system behavior deviate from observed ecosystem behavior. This can occur when people (1) fail to anticipate change in ecosystems; (2) fail to influence ecosystem behavior as intended; or (3) discover something about an ecosystem that runs counter to accepted knowledge. We develop a conceptual model that captures the interactions between social and ecological processes that lead to these events and examine two types of drivers that contribute to surprise: underlying driving forces and proximate causes. Our definition of ecological surprise inherently acknowledges that, to be surprising, there must be human observers to the ecological occurrence who have expectations about ecosystem behavior. To explore this dimension, we draw on social science perspectives to understand the ways in which human expectations of ecosystems are influenced by social networks, heuristics, and mental models. We use a case study to demonstrate how our integrated conceptualization of ecological surprise provides a systematic way of examining these events. Our integration of these perspectives enables us to better synthesize social and ecological knowledge of these events, and encourages ecologists to critically reflect on how they, as scientists, formulate and reformulate expectations of ecosystem behavior.

Key words: discovery; ecosystem; expectations; social systems; social–ecological systems; unexpected change.

Received 24 April 2017; revised 12 September 2017; accepted 3 October 2017. Corresponding Editor: Ginger R. H. Allington.

Copyright: © 2017 Filbee-Dexter et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** kfilbeedexter@gmail.com

INTRODUCTION

The world is currently experiencing considerable losses of natural resources, reductions in biodiversity, increased frequency of extreme events, and collapse in natural systems (IPCC 2014). As the extent and intensity of human impacts on ecosystems increase (Hoekstra et al. 2005, Halpern et al. 2015) and the capacity of ecosystems to absorb these impacts dwindles (Folke et al. 2004), unanticipated behavior in ecological systems—or surprises—is likely to become more common (Magnuson 1990, Scheffer et al. 2001, Drijfhout et al. 2015). The ways in which humans cope with change in natural systems has emerged as a key question in ecology, and the term “ecological surprise” has become increasingly used by researchers studying these dynamics (Scheffer et al. 2001, Williams and Jackson 2007, Dakos et al. 2015). Some examples of ecological surprise include collapse of coastal fisheries (Hilborn et al. 2003), sudden state change during eutrophication of lakes, outbreaks of insects causing widespread mortality of old-growth forests (Safranyik and Wilson 2007), severe forest fires in South America, the accelerated loss of Arctic sea ice compared to model predictions (AMAP 2017), and the return of wolves to Eastern Germany after more than 100 yr of extirpation (Gross 2008, 2010). Here, we define ecological surprise as a situation where human expectations of natural system behavior deviate from observed ecosystem behavior (King 1995, Gunderson 2003, Doak et al. 2008, Lindenmayer et al. 2010).

As the concept of ecological surprise involves both ecosystem behavior and the expectations that people have of these systems, it is therefore best understood from an interdisciplinary perspective that considers both the social and ecological dimensions of these events. Despite its increasing use by ecologists, the notion of ecological surprise is seldom explicitly developed in the literature, and researchers often employ divergent meanings, language, and interpretations in their application of this concept, which limits our ability to synthesize knowledge of these events (Lindenmayer et al. 2010).

The aim of this paper was to synthesize what ecological surprise has meant to ecologists studying these events. To this end, we (1) review the

development of this concept in ecology and beyond, (2) propose a core definition of ecological surprise and develop a conceptual model that captures the interactions between social and ecological processes during these events, and (3) review key concepts and perspectives from social and environmental sciences that describe the social dimensions of our definition of surprise. We apply our conceptual model to the Atlantic cod collapse and conclude with identifying gaps in our knowledge and highlighting strategies for future research.

THE DEVELOPMENT OF THE CONCEPT OF SURPRISE IN ECOLOGY

Ecologists have traditionally viewed surprise as an outcome of the scientific process that requires them to expand, reject, or revise their views of nature (Doak et al. 2008). Consequently, ecologists often use the term “surprise” to describe unexpected findings about the natural environment (Lindenmayer et al. 2010) or experimental results that are not explainable or predictable within existing theory (Gross 2010). Holling (1986) noted that “[s]urprises occur when causes turn out to be sharply different than was conceived, when behaviours are profoundly unexpected, and when action produces a result opposite to that intended, in short, when perceived reality departs qualitatively from expectation.” Doak et al. (2008) described surprise as a situation “when an experienced biologist with clear, well-informed expectations faces outcomes or patterns that strongly contradict these expectations.” Magnuson (1990) explored how time lags in ecological systems separate cause and effect, which can make it difficult to interpret or predict change in the natural world. The concepts of predictability and stability of natural systems are intrinsic to early discussions of ecological surprise. For many ecologists, unpredictable events are simply a part of nature, and observations of random or stochastic behavior are not that surprising. In the same way, a natural system that is purely deterministic and predictable for a given observer contains no surprises.

Another connotation of ecological surprise is the emergence of new information that strongly contradicts current knowledge or theory (Kates and Clark 1996, Doak et al. 2008, Gross 2010). A

classic example was the work by Paine (1966), which demonstrated that a single keystone species could influence an ecosystem far beyond its relative size or abundance, challenging the dominant view at the time that ecosystems were made up of multiple equally important components (Mills et al. 1993). Not all ecological discoveries qualify as surprises. Today, a discovery of a new marine species during a deep-sea research cruise would not be very surprising; in fact, it would probably conform to the expectations of most ecologists familiar with these habitats. For new knowledge to be surprising, it must also trigger awareness of an ecologist's ignorance of key dynamics, events, or processes (Magnuson 1990), or highlight phenomenon that occurs regularly under a set of definite circumstances (Gross 2010). In this way, ecological surprises can be beneficial, creating opportunity for positive change or generation of knowledge.

Some ecologists also use the term "surprise" to describe a sudden regime shift to an alternative community state (Paine et al. 1998). During these events, an ecosystem is pushed past a critical threshold where it reorganizes into a new state maintained by processes or feedbacks that resist further change or recovery (e.g., shift from clear lake to a turbid lake due to addition of nutrients; Scheffer et al. 2001). Here, ecological surprise can be attributed to the initial unexpected change in an ecosystem's fundamental character (Paine et al. 1998).

Finally, there have been several attempts to create a typology and methodology of surprise to identify and categorize these events in ecology and other disciplines (reviewed by Streets and Glantz 2000). Doak et al. (2008) classified ecological surprise into three general categories: (1) dynamic surprises, defined as unexpected changes in community abundance or composition; (2) pattern-based surprises, defined as deviations from spatial or temporal patterns of change; and (3) intervention-based surprises, defined as unexpected dynamics arising from management or human perturbations. Kates and Clark (1996) separate surprise into (1) rare events with serious consequences, (2) common events that elude detection/prevention, (3) unexpected consequences of human action, and (4) expected but mistakenly attributed consequences of human actions. Outside of ecology, Brooks (1986) described three

types of surprise: (1) discrete events that are not expected, (2) discontinuities of long-term trends, and (3) sudden public awareness of new information. Schneider et al. (1998) distinguish between strict and imaginable surprise, the former referring to those events that are unknown, unexpected, and truly unforeseen and the latter to "events or processes that depart from the expectations of some definable community."

THE DEVELOPMENT OF ECOLOGICAL SURPRISE IN OTHER DISCIPLINES

Environmental scientists, researchers, and managers studying social-ecological systems often apply the term "ecological surprise" differently from ecologists. They commonly use it to describe unanticipated consequences of human use or intervention in natural systems. King (1995) proposed that "ecological surprise occurs when humankind creates unexpected, and irreversible changes in the natural environment." Gunderson (2003) defined surprise as "a qualitative disagreement between ecosystem behaviour and a priori expectations" that occurred "in managed systems." Holling (1986) held that "surprise concerns both the natural system and the people who seek to understand causes, to expect behaviours, and to achieve some defined purpose by action." In this framework, ecological surprise occurs when the expectations of people creating policy, managing, or using resources from ecological systems are not met, for example, when a manager establishes a marine protected area expecting to see recovery of a coral reef, but no change occurs (Micheli et al. 2004, Guarderas et al. 2011), or when a governance system sets a quota for sustainable harvest of a fishery and the stock collapses (Hutchings 2000). Here, ecological surprise can be viewed as a failure to control or influence ecological behavior to produce a desired or intended outcome. In this context, the implications of ecological surprise extend beyond ecological consequences to also include losses of ecosystem services and skepticism toward science or management.

Environmental scientists and researchers studying social-ecological systems have often focused on understanding the social dimensions of ecological surprise, including the role of management strategies during unexpected ecological change,

the ways in which observers formulate expectations of natural systems, and how these expectations differ within and across societies (e.g., Berkes et al. 2000, Liu et al. 2007, An 2012). The framing of surprise by these researchers can be difficult to combine with ecological perspectives, because their frameworks, results, and ideas cannot always be applied to surprising events in ecosystems that are not closely linked to social systems (likely because they are conducting research in places where ecosystems are governed by humans or providing services to society). This highlights the need for a definition of surprise that enables synthesis across these diverse perspectives.

A WORKING DEFINITION OF ECOLOGICAL SURPRISE

Our definition aims to unify these many understandings of the term “ecological surprise” into a common concept (Holling 1986, Gunderson 2003). As previously stated, we define ecological surprise as a situation where human expectations or predictions of ecosystem behavior deviate from observed ecosystem behavior. Our definition is conceptually simple in that it requires (1) a human expectation of ecosystem behavior and (2) a significant deviation from that expectation. Surprise is necessarily subjective because it is related to the expectations of the observer (Itti and Baldi 2009). As Gross (2010) states: “A surprise is only a surprise if it is

noticed by the holder of the beliefs it contradicts.” Defined in this way, an ecological surprise is a possible outcome of an interaction between society and natural systems. Ecological surprise can be used to make connections between the complex mechanisms and processes that drive unexpected ecological behavior, and the multiple factors and conditions that determine how societies interpret and form expectations of ecosystems (sensu Stedman 2016).

Importantly, in this definition of surprise, ecosystems can deviate from human expectations in many ways and still fit within our concept. To illustrate this, we show three examples of ecological surprise that describe different ways that an ecosystem can deviate from a human expectation, where the actual and expected behaviors are represented as realized and predicted averages of a time series (Fig. 1). In the first example, the observer within the human system failed to anticipate a sudden change in the ecological system (Fig. 1a). In the second example, the social system failed to influence ecosystem behavior as intended for human use or intervention (Fig. 1b). In the third example, a new discovery about an ecosystem state emerged that ran counter to previous knowledge (Fig. 1c). Other unexpected ecosystem behaviors may include, but are not limited to, linear change, large shocks, new processes or components, or altered variability (these behaviors could be captured similarly to Fig. 1a). Our definition differs from previous

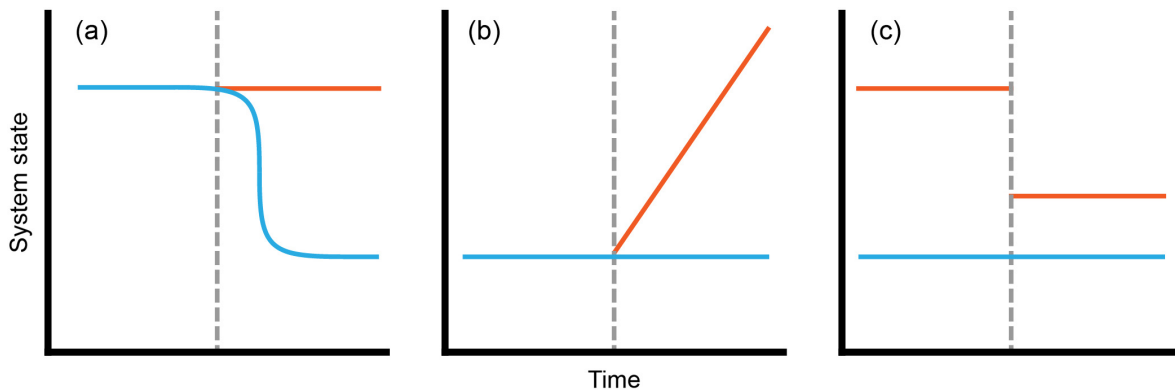


Fig. 1. Three examples of ecological surprise that describe different ways that an ecosystem (lower blue line) can deviate from a human expectation (upper orange line). Surprise (gray dashed line) can occur when people (a) fail to anticipate change in ecosystems; (b) fail to influence ecosystem behavior; or (c) discover something about an ecosystem that runs counter to accepted knowledge. Surprise is indicated by the magnitude of divergence between blue and orange lines over time.

typologies because, instead of classifying these events into different types of ecological surprise, we focus on the overarching dynamic, which is a deviation from human expectation.

Two broad types of drivers can contribute to unexpected ecological behaviors: underlying driving forces and proximate causes (Fig. 2). Underlying drivers occur well before the surprising event, but set the stage for unexpected ecosystem behavior. Underlying drivers often result in a gradual degradation relative to historic baselines (Jackson et al. 2001) or an erosion of resilience that brings an ecosystem close to a critical threshold, making it more susceptible to sudden change (Scheffer et al. 2001, Hicks et al. 2016, Österblom et al. 2016). Proximate causes are changes to, or impacts on, an ecosystem that occur in the period immediately before surprise. Proximate causes of an unexpected ecological behavior can include abiotic events such as strong storms and climatic variability; altered

biological processes, species' invasions, synergism between multiple stressors, new dynamics that make the ecosystem resistant or vulnerable to change, or perturbations that push the system over a critical threshold; and human actions (intentional or otherwise) to modify the ecosystem. For some types of ecosystem behavior, the period before surprise can be signaled by increased variability or slow recovery from small perturbations, which occurs when an ecosystem approaches a critical threshold for an ecological regime shift (Scheffer et al. 2001, Dakos et al. 2015). Humans are generally not well adapted to consider the passage of time, and we tend to focus on the recent past or present in our interpretation of ecological events (Magnuson 1990). As a result, surprise is often attributed to proximate drivers, but they can simply be the final straw in a series of impacts or actions altering the ecosystem over a much longer period (Jackson et al. 2001).

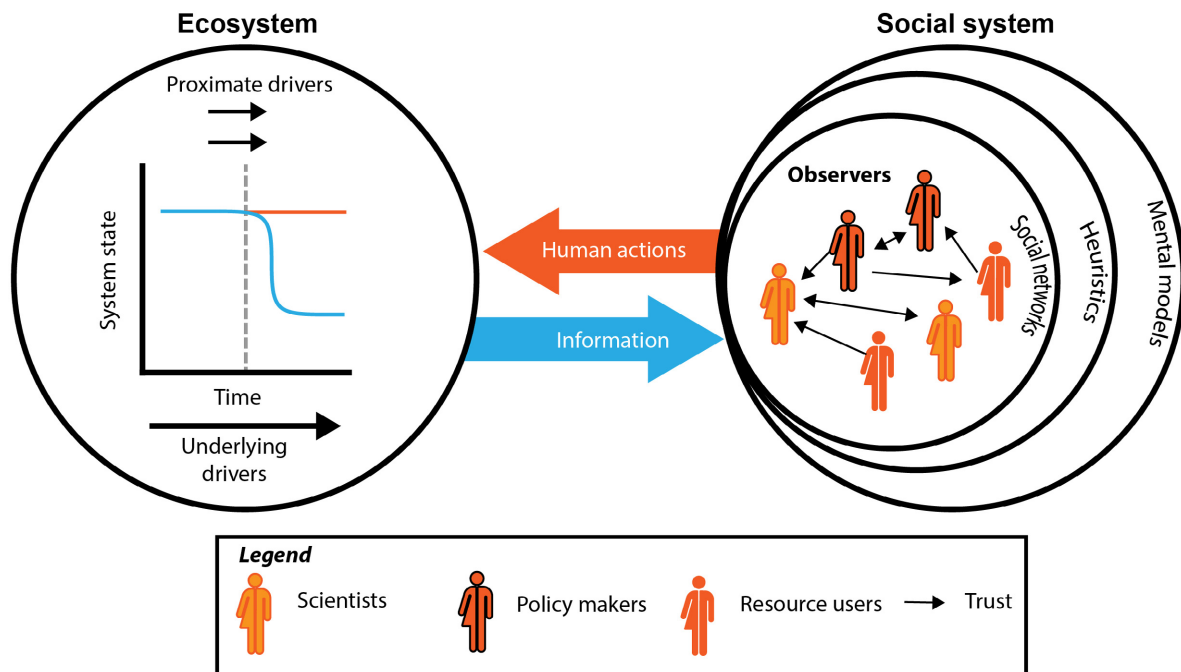


Fig. 2. A conceptual model depicting surprise as an outcome of the interaction(s) between natural and social systems. The ecosystem is shown undergoing unexpected behavior (in this case, a regime shift to a new state; see Fig. 1) due to a combination of underlying and proximate drivers (black arrows). The social system is composed of various observers (scientists, resource users, and policy makers) that form expectations of natural systems based on their social network, heuristics, and mental models. The blue arrow represents the flow of information from natural systems to human observers, and the orange arrow represents the returning influence of human actions on natural systems.

Social–ecological systems undergo a continuous cycle of surprise, reorganization, transformation, or adaptation, where people are constantly encountering new behaviors in ecological systems and then closing the gap between reality and expectation as they modify their understanding of the system. In our concept, the magnitude of surprise is represented by the difference between human expectation and the observed state of the system (the gap between the social and ecological systems in Fig. 1). Over time, the gap between people’s expectations and ecosystem behavior can shrink as adaptation and learning (experience) brings expectations back in line with ecological reality. For example, we now know that ecosystems can be stabilized by feedback mechanisms that prevent subsequent recovery (Biggs et al. 2009). With this knowledge, we should now not be surprised if a fertilized lake suddenly becomes overgrown by algae and anoxic, or if an old monoculture stand of pine trees catches fire, and that these systems remain in the altered state after the initial disturbance ceases (Scheffer et al. 2001).

EXPLORING THE SOCIAL DIMENSIONS OF ECOLOGICAL SURPRISE

A social–ecological systems perspective emphasizes the inherent interdependence and two-way feedbacks that exist between humans and the environment (Fig. 2; Berkes and Folke 1998). Here, we draw attention to the flow of information (e.g., through ecosystem monitoring or changes in ecosystem services) from natural systems to multiple human observers (e.g., scientists, resource users, policy makers; Fig. 2). This information, coupled with human expectations and experiences, informs decisions to act and dictate what actions are taken. In turn, this suite of actions impact ecosystems.

The social dimensions of our definition of ecological surprise deal with (1) the ways in which observers formulate expectations regarding ecosystem behavior and (2) why these expectations differ within and across societies. The social sciences provide a range of disciplinary perspectives (e.g., cognitive psychology, sociology, behavioral economics) for examining these dimensions (see Bennett et al. [2017] for an example of the contributions of the social sciences for conservation). Integration of these concepts should clarify how

ecologists, as experts, formulate and reformulate expectations of ecosystems using their individual experiences, ecological knowledge, and accepted theory. Social science perspectives can also be used to understand what actions are taken to respond and navigate ecological surprise (Bennett et al. 2017). However, here we focus our discussion on understanding the ways in which observers formulate expectations regarding ecosystem behavior and why these expectations differ within and across societies.

To highlight key perspectives and insights that can inform our understanding of ecological surprise, we draw upon the literature from risk perception, including both natural hazards (e.g., Eiser et al. 2012) and ecological risk (e.g., Slimak and Dietz 2006, Willis and DeKay 2007). We understand perception as “the way an individual observes, understands, interprets, and evaluates a referent object, action, experience, individual, policy, or outcome” (Bennett 2016). Here, we are particularly interested in explaining the differences in how individuals perceive ecological surprise (see Slimak and Dietz 2006). To this end, we explore how, in addition to direct observations of an ecological system, people’s perceptions and expectations regarding ecosystem behavior (Berkes et al. 2008, Ostrom 2009) are influenced by social networks, heuristics, and mental models, along with their complex interactions. We focus on social networks, heuristics, and mental models because they have been shown to underpin people’s perceptions and predictions of risk (Eiser et al. 2012). These three elements enable us to explore (1) how human interactions and trust influence risk perception (i.e., social networks); (2) how people’s conceptions of reality are embedded within, and influenced by, their broader societies (i.e., mental models); and (3) how knowledge and experience influence people’s reception of information and decisions to act (i.e., heuristics).

Social networks and trust

Social networks and relations among observers influence their expectations of ecosystem behavior and how they perceive surprise. Networks play a role in spreading information and ideas about expected ecosystem behavior, and observers cognitively process the information they receive from networks (Lubell et al. 2011). As such, there is a constant interplay between

information transmission, individual cognition, and the construction of expected ecosystem behavior. Accordingly, the same flow of information from natural systems will carry different amounts of surprise for different observers, or even for the same observer taken at different times (Itti and Baldi 2009; Fig. 2). Of particular note in regard to social networks is the role of trust (Henry and Dietz 2011). People are more likely to form expectations using information they receive from people they trust (Eiser et al. 2012). Trust has multiple dimensions, but importantly people accept information from perceived subject experts and further believe that experts will not use their insights to disrupt social well-being (Eiser et al. 2012). As such, patterns of expectations across a community or population are often partially contingent upon the patterns of trust found within that community or population. For example, some communities trust scientists and managers studying and regulating natural systems to monitor key ecological variables, explain current dynamics, or generate realistic predictions of future behavior. However, in some situations, personal biases or different mental models of the system can cause an observer's expectation to deviate from expert opinion.

Heuristics

Kahneman and Tversky (1979) have shown how people use cognitive reference points to judge the nature or severity of a situation, and knowledge and experience influence these cognitive reference points. In the context of ecological surprise, people's knowledge and experience influence what is perceived as normal or unsurprising behavior (Schneider et al. 1998; Fig. 2). Closely related is the concept of heuristics. Heuristics form the basis for human decision making in the context of risk and uncertainty, and they ultimately allow people to make simple, potentially sub-optimal decisions quickly in the face of limited or imperfect information (Gigerenzer et al. 2011). For example, the availability heuristic proposes "events are judged to be more probable if imagining or recalling similar instances from memory is easier" (Eiser et al. 2012). This has led people to interpret more memorable events as more likely and less surprising regardless of the observed probability of a certain event occurring (Eiser et al. 2012). For

example, a severe hurricane is considered more likely to hit New Orleans compared to other areas of the Gulf Coast, even though models show that these events have an equal probability of occurrence. Likewise, the outcome of the memorable first trial in a series of experiments will have a stronger influence on a researcher's prediction of the effect size compared to the outcome of the second or third trial.

Mental models

People also have overarching mental models, or "personal, internal representations of external reality that people use to interact with the world" (Jones et al. 2011; Fig. 2) that are likely to influence perceptions of ecological surprise. Mental models are formed based on experience and access to information regarding ecosystem behavior, and they act as a cognitive filter for interpreting and storing new information (Chen 2011, Jones et al. 2011, Stier et al. 2016). Mental models also constrain the ability of individuals to accept information that challenges their current conception of reality, which leads to confirmation biases (Klayman and Ha 1989). In the context of ecological surprise, mental models can potentially cause people to ignore early warning signs and thus be more surprised in light of impending ecosystem behavior (Chen 2011, Jones et al. 2011). For example, ecologists or managers may unconsciously fit new information into their current mental model of the system and will be surprised if the ecosystem changes in a way that is contrary to this understanding.

UNDERSTANDING SURPRISE: APPLICATIONS AND STRATEGIES

Atlantic cod collapse: case study

The way in which we deal with uncertainty in social-ecological systems depends on how social actors adapt and learn from ecological surprise (Streets and Glantz 2000). To illustrate how our framework provides a systematic way of identifying and understanding ecological surprise, we apply it to the Atlantic cod collapse in eastern Canada. This case study consists of two unexpected events. The first occurred in the early 1990s, when the cod stock dramatically declined (Myers et al. 1997). In this instance, the unexpected ecological behavior was an abrupt shift

(collapse) where the ecological system deviated from the managerial expectations of how continued harvest should control variability in this resource (Fig. 1a). Various ecological and social mechanisms were responsible for this deviation. Initiatives to intensify the fishery did not account for altered population structure (proximate drivers) or historic overexploitation (underlying driver), and the stock declined, resulting in the immediate loss of catch and income (Myers et al. 1997, Hamilton et al. 2004). We can quantify ecological surprise as the difference between the predicted amount of cod biomass (based on the percent allocated as total allowable catch) and the actual cod biomass (calculated using catch per unit effort, government surveys, and/or ecological models). The expectations of many social actors were that cod was a robust resource that could withstand intensified exploitation; this strongly held belief was derived from observations on the impact of foreign fishing fleets, long-term records of variation in historical cycles of highs and lows in stock abundance, and trust in traditional management strategies (underlying drivers). In contrast, many fishers and scientists directly using or monitoring the resource were not surprised by the collapse, but warned people of the negative impacts of offshore intensification and the trends of declining catch per unit effort in the period leading up to the event (Finlayson 1994).

The second surprise occurred after managers closed the fishery, when quick stock recovery was expected but did not occur (Finlayson and McCay 1998). Again, we can quantify this surprise as the difference between the amount of cod biomass at the time of the closure and the biomass before the collapse (expected recovery level). In this case, the ecological surprise was a lack of ecosystem recovery and involved a failure of the management system to anticipate the response of the natural system to constrain cod stock recovery (Fig. 1b). Specifically, management initiatives did not account for feedback mechanisms that reinforced the new invertebrate-dominated state and suppressed cod recruitment (Myers et al. 1997). From a social perspective, this outcome challenged many core assumptions regarding fishery management and led to a re-evaluation of these strategies (Myers et al. 1997). The cod collapse affected the livelihoods of 35,000 fishers and fish-plant workers and lost \$200 million in annual revenue (DFO

2004). The prolonged collapse of the coastal economy and loss of livelihoods also provided a learning opportunity for people managing fisheries around the world and is an iconic example of over-exploitation and destructive harvesting practices (Finlayson and McCay 1998, Worm et al. 2009).

COPING WITH ECOLOGICAL SURPRISE

One approach to manage surprise is to attempt to identify and prevent these events. However, it is often only by gaining temporal perspective or experience that we can identify triggers and strategies that would have avoided a crisis. We propose that a better approach is identifying strategies to cope with unavoidable surprise. For example, scenario planning by implementing policy that can be easily reversed or modified if the short-term results or emerging information (from multiple different actors) is inconsistent with people's original expectations (Schultz et al. 2015). Managers can also plan for ecological surprise by focusing on a diversity of approaches, functions, and taxa in their recovery strategies (Hilderbrand et al. 2005). Recent work has demonstrated that governance systems can better respond to surprise if they incorporate uncertainty in their predictions of natural systems by employing the precautionary principle (Doak et al. 2008), actively managing for thresholds, or using adaptive management strategies (Armitage et al. 2009, Horan et al. 2011, Kelly et al. 2015). Designs for organizational structures and processes in the management of natural systems should also include mechanisms for multiple people to identify and respond to unexpected events. A well-known example of this is the red cord in the Toyota assembly line. In this system, every worker has the ability, even the responsibility, to stop the assembly line by pulling the cord if a surprise threatens the overall performance. Pulling the cord prompts quick action to repair the system (Huff et al. 2006). In a similar way, policy makers, scientists, managers, industries, civil society groups, and government agencies should all have mechanisms to identify and respond to unexpected behavior in ecosystems.

The manner in which ecologists define and emphasize uncertainty in their predictions remains a contentious issue that can compromise effective communication of science to managers,

policy makers, and the public (Kinzig and Starrett 2003). Uncertainty can be used as an excuse for inaction (Gunderson 2003). However, there are several examples where human institutions successfully account for uncertainty. In the insurance industry, action to mitigate surprise can be prompted if stakeholders are provided with realistic estimates of the likelihood of extreme events and the costs of inaction (Kinzig and Starrett 2009). In the same way, ecologists can provide information on the frequency and costs of ecological surprise, and predictions of ecological behavior with clearly communicated uncertainty and underlying assumptions that will be invaluable to societies implementing strategies to sustain their resource systems.

CONCLUSIONS

Societies and scientists should prepare to encounter new and unexpected behavior in natural systems. To better deal with ecological surprise, ecologists must get better at prediction, or at least understanding when and why predictions work or not (Watts 2014). This is a difficult task. Ecosystems are complex, with multiple known and unknown components, and hierarchical interactions between components which all vary in time and space (Taylor 2010). In addition, new challenges arising from shifting environmental conditions, species invasions, and human impacts are likely to modify these interactions and system components. These elements are occurring over a range of temporal scales and make it extremely difficult to predict future ecological behavior (Taylor 2010). Systematically examining the underlying and proximate drivers of surprise across multiple ecosystems could be a powerful way to identify common drivers or mechanisms that lead to ecological surprise. While this paper does not explicitly deal with how to improve ecological predictions, there is considerable research on this topic (e.g., Gunderson 2001, Petchey et al. 2015). Increasing the accuracy of prediction requires long-term ecological monitoring, modeling, and experimental testing of theory, which should be a priority moving forward.

Incorporating human systems into current research on ecosystem stability is a key challenge and will be a crucial aspect to consider when seeking to better address challenges of ecological

surprises. Use of an integrative conceptual foundation for ecological surprise by ecologists will enable managers and researchers in other disciplines to better incorporate information on unexpected ecological dynamics into design and management strategies. Current theory on these social dynamics is diverse and sometimes conflicting, making it difficult for ecologists to use these perspectives in their research. Further clarity is needed on how knowledge and belief systems influence the ways in which we generate expectations of ecosystem behavior. Quantitative and qualitative data on how management can contribute or successfully respond to ecological surprise are needed. We also lack a quantitative unit of ecological surprise and so the amount remains vague and elusive, often precluding mathematical analysis (Itti and Baldi 2009). Clear benefits lie at exploring the intersection of ecology and society. Successful integration can come from developing common conceptual models that bridge current ecological and social theory. This bridging is essential if we are to find solutions to pressing environmental problems in a rapidly changing world.

ACKNOWLEDGMENTS

We thank Matthew Bass for his invaluable help with the conception of this manuscript. We also thank Peter R. Leavitt and Robert E. Scheibling for helpful comments on earlier drafts. The authors are part of an interdisciplinary graduate research pursuit funded by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the National Science Foundation, DBI-1052875. SESYNC supports collaborative research on human and ecological systems.

LITERATURE CITED

- AMAP. 2017. Snow, water, ice and permafrost in the Arctic (SWIPA): climate change and the cryosphere. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.
- An, L. 2012. Modeling human decisions in coupled human and natural systems: review of agent-based models. *Ecological Modelling* 229:25–36.
- Armitage, D. R., et al. 2009. Adaptive co-management for social–ecological complexity. *Frontiers in Ecology and the Environment* 7:95–102.
- Bennett, N. J. 2016. Using perceptions as evidence to improve conservation and environmental management. *Conservation Biology* 30:582–592.

- Bennett, N. J., et al. 2017. Conservation social science: understanding and integrating human dimensions to improve conservation. *Biological Conservation* 205:93–108.
- Berkes, F., J. Colding, and C. Folke. 2008. Navigating social-ecological systems: building resilience for complexity and change. Cambridge University Press, Cambridge, UK.
- Berkes, F., and C. Folke. 1998. Linking social and ecological systems for resilience and sustainability. Pages 1–25 in F. Berkes, C. Folke, and J. Colding, editors. *Linking social and ecological systems management practices and social mechanisms for building resilience*. Cambridge University Press, Cambridge, UK.
- Berkes, F., C. Folke, and J. Colding. 2000. Linking social and ecological systems: management practices and social mechanisms for building resilience. Cambridge University Press, Cambridge, UK.
- Biggs, R., S. R. Carpenter, and W. A. Brock. 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences* 106:826–831.
- Brooks, H. 1986. The typology of surprises in technology, institutions and development. *Sustainable development of the biosphere*. Pages 325–347 in W. C. Clark and R. E. Munn, editors. *Sustainable development of the biosphere*. IIASA, Laxenburg, Austria.
- Chen, X. 2011. Why do people misunderstand climate change? Heuristics, mental models and ontological assumptions. *Climatic Change* 108:31–46.
- Dakos, V., S. R. Carpenter, E. H. van Nes, and M. Scheffer. 2015. Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B* 370:20130263.
- DFO. 2004. Fish landings and landed values. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.
- Doak, D. F., et al. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? *Ecology* 89:952–961.
- Drijfhout, S., S. Bathiany, C. Beaulieu, V. Brovkin, M. Claussen, C. Huntingford, M. Scheffer, G. Sgubin, and D. Swingedouw. 2015. Catalogue of abrupt shifts in Intergovernmental Panel on Climate Change climate models. *Proceedings of the National Academy of Sciences USA* 112:E5777–E5786.
- Eiser, J. R., A. Bostrom, I. Burton, D. M. Johnston, J. McClure, D. Paton, J. Van Der Pligt, and M. P. White. 2012. Risk interpretation and action: a conceptual framework for responses to natural hazards. *International Journal of Disaster Risk Reduction* 1:5–16.
- Finlayson, A. C. 1994. Fishing for truth: a sociological analysis of northern cod stock assessments from 1977 to 1990. *Social and economic studies* no. 52. Institute of Social and Economic Research, Memorial University of Newfoundland, St. John's, Newfoundland, Canada.
- Finlayson, C. A., and B. J. McCay. 1998. Crossing the threshold of ecosystem resilience: the commercial extinction of northern cod. Pages 311–338 in F. Berkes, C. Folke, and J. Colding, editors. *Linking social and ecological systems management practices and social mechanisms for building resilience*. Cambridge University Press, Cambridge, UK.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- Gigerenzer, G., R. Hertwig, and T. Pachur. 2011. *Heuristics: the foundations of adaptive behaviour*. Oxford University Press, New York, New York, USA.
- Gross, M. 2008. Return of the wolf: ecological restoration and the deliberate inclusion of the unexpected. *Environmental Politics* 17:115–120.
- Gross, M. 2010. *Ignorance and surprise: science, society, and ecological design*. MIT Press, Cambridge, Massachusetts, USA.
- Guarderas, A. P., S. D. Hacker, and J. Lubchenco. 2011. Ecological effects of marine reserves in Latin America and the Caribbean. *Marine Ecology Progress Series* 429:219–225.
- Gunderson, L. H. 2001. *Panarchy: understanding transformations in human and natural systems*. Island Press, Washington, D.C., USA.
- Gunderson, L. H. 2003. Adaptive dancing: interactions between social resilience and ecological crises. Pages 33–52 in F. Berkes, J. Colding, and C. Folke, editors. *Navigating social-ecological systems: building resilience for complexity and change*. Cambridge University Press, Cambridge, UK.
- Halpern, B. S., et al. 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications* 6:7615.
- Hamilton, L. C., R. L. Haedrich, and C. M. Duncan. 2004. Above and below the water: social-ecological transformation in Northwest Newfoundland. *Population and Environment* 25:195–215.
- Henry, A. D., and T. Dietz. 2011. Information, networks, and the complexity of trust in commons governance. *International Journal of the Commons* 5:188–212.
- Hicks, C. C., L. B. Crowder, N. A. Graham, J. N. Kittinger, and E. L. Cornu. 2016. Social drivers forewarn of marine regime shifts. *Frontiers in Ecology and the Environment* 14:252–260.
- Hilborn, R., T. A. Branch, B. Ernst, A. Magnusson, C. V. Minte-Vera, M. D. Scheuerell, and J. L. Valero.

2003. State of the world's fisheries. *Annual Review of Environment and Resources* 28:359–399.
- Hilderbrand, R. H., A. C. Watts, and A. M. Randle. 2005. The myths of restoration ecology. *Ecology and Society* 10:19.
- Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8:23–29.
- Holling, C. S. 1986. The resilience of terrestrial ecosystems: local surprise and global change. Sustainable development of the biosphere. Cambridge University Press, Cambridge, UK.
- Horan, R. D., E. P. Fenichel, K. L. Drury, and D. M. Lodge. 2011. Managing ecological thresholds in coupled environmental–human systems. *Proceedings of the National Academy of Sciences* 108:7333–7338.
- Huff, A., D. Tranfield, and J. E. van Aken. 2006. Management as a design science mindful of art and surprise a conversation between Anne Huff, David Tranfield, and Joan Ernst van Aken. *Journal of Management Inquiry* 15:413–424.
- Hutchings, J. A. 2000. Collapse and recovery of marine fishes. *Nature* 406:882–885.
- IPCC. 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Itti, L., and P. Baldi. 2009. Bayesian surprise attracts human attention. *Vision Research* 49:1295–1306.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
- Jones, N. A., H. Ross, T. Lynam, P. Perez, and A. Leitch. 2011. Mental models: an interdisciplinary synthesis of theory and methods. *Ecology and Society* 16:46.
- Kahneman, D., and A. Tversky. 1979. Prospect theory: an analysis of decision under risk. *Econometrica: Journal of the Econometric Society* 47:263–291.
- Kates, R. W., and W. C. Clark. 1996. Environmental surprise: Expecting the unexpected? *Environment* 38:6–34.
- Kelly, R. P., A. L. Erickson, L. A. Mease, W. Battista, J. N. Kittinger, and R. Fujita. 2015. Embracing thresholds for better environmental management. *Philosophical Transactions of the Royal Society B* 370:20130276.
- King, A. 1995. Avoiding ecological surprise: lessons from long-standing communities. *Academy of Management Review* 20:961–985.
- Kinzig, A., and D. Starrett. 2003. Coping with uncertainty: a call for a new science-policy forum. *Ambio* 32:330–335.
- Klayman, J., and Y.-W. Ha. 1989. Hypothesis testing in rule discovery: strategy, structure and content. *Journal of Experimental Psychology* 5:596–604.
- Lindenmayer, D. B., G. E. Likens, C. J. Krebs, and R. J. Hobbs. 2010. Improved probability of detection of ecological “surprises”. *Proceedings of the National Academy of Sciences USA* 107:21957–21962.
- Liu, J., et al. 2007. Complexity of coupled human and natural systems. *Science* 317:1513–1516.
- Lubell, M. N., G. Robins, and P. Wang. 2011. Policy coordination in an ecology of water management games. Paper 22. 4th Annual Political Networks Conference and Workshops, Ann Arbor, Michigan, June 14, 2011.
- Magnuson, J. 1990. Long-term ecological research and the invisible present. *BioScience* 40:495–501.
- Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. 2004. Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications* 14:1709–1723.
- Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219–224.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications* 7:91–106.
- Österblom, H., B. I. Crona, C. Folke, M. Nyström, and M. Troell. 2016. Marine ecosystem science on an intertwined planet. *Ecosystems* 20:54–61.
- Ostrom, E. 2009. A general framework for analyzing sustainability of social-ecological systems. *Science* 325:419–422.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1:535–545.
- Petchey, O. L., M. Pontarp, T. M. Massie, and S. Kéfi. 2015. The ecological forecast horizon, and examples of its uses and determinants. *Ecology Letters* 18:597–611.
- Safranyik, L., and B. Wilson. 2007. The mountain pine beetle: a synthesis of biology, management and impacts on lodgepole pine. Canadian Forest Service, Victoria, Canada.
- Scheffer, M., S. Carpenter, J. Foley, and C. Folke. 2001. Catastrophic shifts in ecosystems. *Nature* 413:519–596.
- Schneider, S. H., B. L. Turner, and H. M. Garriga. 1998. Imaginable surprise in global change science. *Journal of Risk Research* 1:165–185.
- Schultz, L., C. Folke, H. Österblom, and P. Olsson. 2015. Adaptive governance, ecosystem management,

- and natural capital. *Proceedings of the National Academy of Sciences USA* 112:7369–7374.
- Slimak, M. W., and T. Dietz. 2006. Personal values, beliefs, and ecological risk perception. *Risk Analysis* 26:1689–1705.
- Stedman, R. C. 2016. Subjectivity and social-ecological systems: a rigidity trap (and sense of place as a way out). *Sustainability Science* 11:891–901.
- Stier, A. C., J. F. Samhouri, S. Gray, R. G. Martone, M. E. Mach, B. S. Halpern, C. V. Kappel, C. Scarborough, and P. S. Levin. 2016. Integrating expert perceptions into food web conservation and management. *Conservation Letters* 10:67–76.
- Streets, D., and M. H. Glantz. 2000. Exploring the concept of climate surprise. *Global Environmental Change* 10:97–107.
- Taylor, P. J. 2010. *Unruly complexity: ecology, interpretation, engagement*. University of Chicago Press, Chicago, Illinois, USA.
- Watts, D. J. 2014. Common sense and sociological explanations. *American Journal of Sociology* 120: 313–351.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5: 475–482.
- Willis, H. H., and M. L. DeKay. 2007. The roles of group membership, beliefs, and norms in ecological risk perception. *Risk Analysis* 27:1365–1380.
- Worm, B., et al. 2009. Rebuilding global fisheries. *Science* 325:578–585.