

OVERVIEW



# Resilience of aquatic systems: Review and management implications

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## Abstract

Our understanding of how ecosystems function has changed from an equilibria-based view to one that recognizes the dynamic, fluctuating, nonlinear nature of aquatic systems. This current understanding requires that we manage systems for resilience. In this review, we examine how resilience has been defined, measured and applied in aquatic systems, and more broadly, in the socioecological systems in which they are embedded. Our review reveals the importance of managing stressors adversely impacting aquatic system resilience, as well as understanding the environmental and climatic cycles and changes impacting aquatic resources. Aquatic resilience may be enhanced by maintaining and enhancing habitat connectivity as well as functional redundancy and physical and biological diversity. Resilience in aquatic socioecological system may be enhanced by understanding and fostering linkages between the social and ecological subsystems, promoting equity among stakeholders, and understanding how the system is impacted by factors within and outside the area of immediate interest. Management for resilience requires implementation of adaptive and preferably collaborative management. Implementation of adaptive management for resilience will require an effective monitoring framework to detect key changes in the coupled socioecological system. Research is needed to (1) develop sensitive indicators and monitoring designs, (2) disentangle complex multi-scalar interactions and feedbacks, and (3) generalize lessons learned across aquatic ecosystems and apply them in new contexts.

**Keywords** Resilience adaptive management · Aquatic · Socioecological system

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## Introduction

The United States' Clean Water Act (CWA) was implemented in 1972 to “restore and maintain the chemical, physical and biological integrity of the Nation’s waters.” Although this law has been highly successful in protecting and restoring many of the Nation’s waters, some areas are still impaired or threatened. For example, point source control efforts implemented under the CWA were very effective in reducing pollutant inputs to US waters, but non-point-source pollution was only indirectly addressed through state water quality standards and the Section 404 dredge and fill permits, which often impact wetlands (Glicksman and Batzel 2010). In addition, since the CWA was written, our understanding of how ecosystems function has evolved. It was once assumed that ecosystems were in equilibria and that degraded systems could be returned to their previous pristine state following the removal of stressors (Adler 2010; Glicksman and Batzel 2010). However, we now recognize that ecosystems are dynamic, fluctuating non-linear systems that may not revert to previous conditions even if stressors

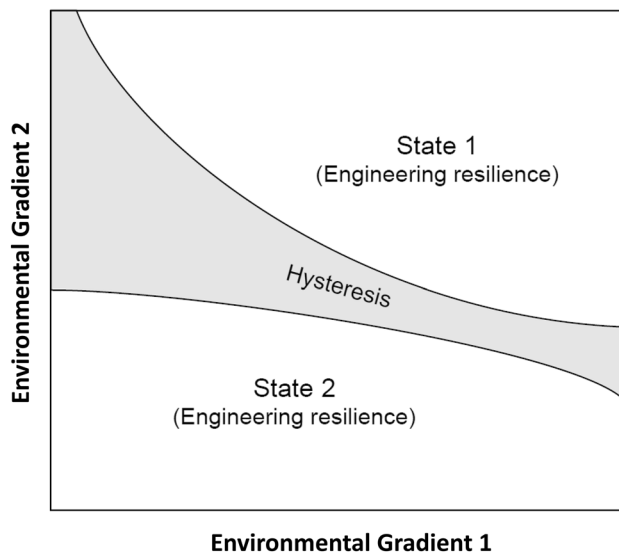
are removed. Realization of this inherent complexity has shown the need to understand and manage waterbodies for system resilience to achieve the ecological integrity goals envisioned in the CWA.

Resilience refers to the ability of systems to absorb changes and disturbance (Holling 1973). Disturbance in this context is defined broadly as anything that perturbs the system (e.g., nutrient enrichment and overharvesting). There are two major types of resilience—engineering and ecological (Table 1). Engineering resilience focuses on the stability of an ecosystem and the speed it reverts to a steady state condition following disturbance (Holling 1996). Ecological resilience focuses on the capacity of an ecosystem to absorb and adapt to disturbances while maintaining its essential structure and function (components and processes) and assumes the existence of multiple stable ecosystem states (Holling 1996). Distinguishing between ecological and engineering

resilience, or whether a change in ecological condition is a regime change may seem inconsequential, but the application of these concepts may have consequences in how systems are managed. Within a given state, there may be environmental declines due to stressors, but if only one state is possible, then recovery is likely if the causative stressors are removed (Fig. 1). If there are multiple states, and the system has transitioned to a new state, then even with removal of stressors, there may not be full or immediate recovery due to hysteresis (Table 1, Fig. 2). Restoration and recovery studies suggest that hysteresis is a common pattern (Duarte et al. 2015) with ecosystems rarely recovering to their previous, undegraded condition (Borja et al. 2010; Lotze et al. 2011; Verdonschot et al. 2013) even when major stressors are reduced or removed. Although ecological resilience is often not recognized until after it is lost, some authors have suggested that engineering resilience may be predictive of

**Table 1** Definition of resilience-related concepts

Concept	Definition	References
Alternate stable states	More than one ecosystem condition (state) possible for a particular set of environmental variables. Associated with abrupt shifts in ecosystems, tipping points, and hysteresis	Oliver et al. (2015)
Cross-scale resilience	Diverse and overlapping function within scales and redundancy of function across scales	Petersen et al. (1998)
Early warning (leading) indicators	Statistical characteristics that allow prediction of a regime shift	Dakos et al. (2012)
Ecological threshold ("tipping point")	Point at which there is an abrupt change in ecological state; may be due to a small change or disturbance	Groffman et al. (2006)
Ecological resilience	Capacity of an ecosystem to absorb and adapt to disturbances while maintaining its essential structure and function and assumes the existence of multiple stable ecosystem states	Holling (1973)
Ecosystem services	Direct and indirect benefits provided to humans from ecosystems	Costanza et al. (1997)
Engineering resilience	Stability of an ecosystem and the speed it reverts to a steady state condition following disturbance. Only one stable state or regime is assumed	Holling (1996)
Functional diversity	Diversity based on species ecological traits (feeding guild, trophic position, etc.) rather than taxonomy	Petchey and Gaston (2006)
Functional redundancy	Species or aspects of the socioecological system perform similar roles	Biggs et al. (2012)
Hysteresis	Forward trajectory not equivalent to the return trajectory between alternate states	Beisner et al. (2003)
Natural capital	Living and non-living components of ecosystems that contribute to people	Guerry et al. (2015)
Panarchy	Hierarchical structure of socioecological systems at multiple spatial and temporal scales characterized by adaptive cycles of growth, accumulation, restructuring, and renewal	Holling (2001)
Regime shift	Ecosystem threshold is crossed due to due to a sudden change in feedbacks; system trajectory moves towards a different attractor (change to an alternative stable state, e.g., shift from clear to turbid water in shallow lakes)	Folke et al. (2004)
Resistance	Capacity of a populations and communities to remain unchanged in the face of disturbance	Angeler and Allen (2016)
Response diversity	Within a given functional group, individual species respond differently to environmental stress, which acts to stabilize the ecological system. Diversity in the spatial distribution of species within a functional group may also contribute	Elmqvist et al. (2003)
Socioecological resilience	Ability of the coupled social and ecological system to retain similar structure, function and feedback mechanisms; considers the importance of multiple scales (panarchy)	Alberti and Marzluff (2004), Walker et al. (2004)

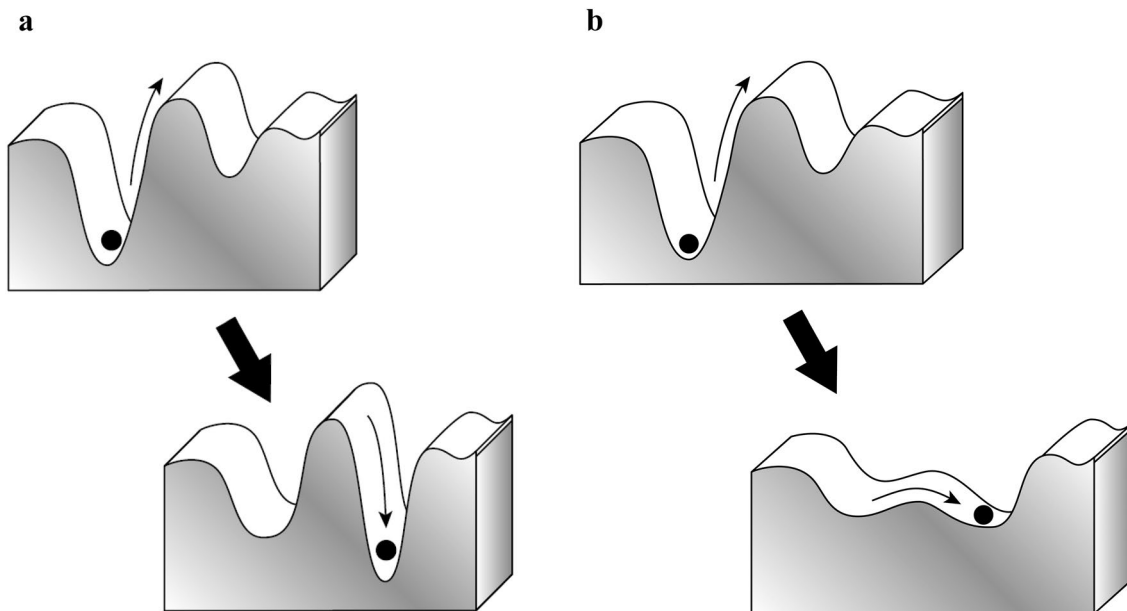


**Fig. 1** Model of resilience adapted from Janssen et al. (2014). Ecological resilience assumes the possibility of multiple ecological states. It is possible to move between these states (regime shifts). Regime shifts can appear to be abrupt and are often characterized by hysteresis, where an ecological trajectory during ecosystem degradation does not match that of ecosystem recovery. This is represented by the grayed area between the two states. Within either state, there may also be disturbance. Engineering resilience focuses on the stability of an ecosystem and the speed it reverts to a steady state condition following disturbance (i.e., within that state). It has been suggested that engineering resilience may provide some insight into its ecological resilience

ecological resilience (Thrush et al. 2009; Scheffer et al. 2015). Also, because engineering resilience is concerned about recovery rates and management practices that enhance recovery, it is particularly relevant for restoration efforts.

A common way to visualize ecological resilience is the ‘cup and ball’ model (Beisner et al. 2003), with the ball representing ecosystem or socioecological state that can exist at any point along the surface of hills and valleys (Fig. 2a). Resilience is represented by the width of the cup, while resistance (Table 1) is represented by the height of the cup. With small perturbations, the ball may be nudged up the walls of the valley but remain in its current regime or state. With increasing perturbation (either internal or external), the ball may cross an ecological threshold (Table 1) into another valley, altering its state. Resistance is high if the ball remains in the valley in the face of these perturbations. Alternately, the landscape itself (environmental or social conditions) may also change (Beisner et al. 2003; Merrill et al. 2018), favoring a new state (Fig. 2b). Because they must overcome strong reinforcing feedback loops, these regime shifts (Table 1) can appear to be abrupt and are often characterized by hysteresis, where an ecological trajectory during ecosystem degradation does not match that of ecosystem recovery.

These multiple ecosystem states (alternate stable states, Table 1) have been demonstrated in a variety of aquatic systems. One classic example is the response of shallow



**Fig. 2** Schematic of ‘ball and cup’ model of resilience. The ball represents the ecosystem or socioecological state that can exist at any point along the surface of hills and valleys. The valleys indicate different regimes, while the arrows indicate variables impacting the population or community directly (e.g., predator removal, overharvesting or completion). The ball may be nudged up the walls of the valley but

remain in its current regime or state with small perturbations. **a** With increasing perturbation (either internal or external; e.g., predator removal, or competition), the ball may be pushed into another valley, altering its state. **b** The landscape itself (environmental conditions) may also change, favoring a new state

lakes to eutrophication. There are at least two stable regimes: the clear water, oligotrophic state and the turbid water, eutrophic state (Carpenter and Cottingham 1997; Carpenter 2003; Scheffer and Carpenter 2003; Zhang et al. 2003; Bayley et al. 2007; Ibelings et al. 2007). Clear water lakes have high ecosystem and recreational value and are characterized by low nutrient inputs, low recycling of phosphorus, and extensive macrophyte beds. These macrophytes are key drivers reinforcing the clear water state (Scheffer et al. 2001; Carpenter 2003; Zhang et al. 2003). Macrophytes remove available nutrients for algal growth and stabilize sediment, providing a positive feedback loop that impedes planktonic algal growth and reduces turbidity (Scheffer et al. 1993; Ibelings et al. 2007). If nutrient loading into a lake exceeds a certain threshold, a different positive feedback loop can be initiated. This leads to a substantial decrease in macrophytes due to algal blooms and sediment resuspension that decreases light availability culminating in a lake tipping into a turbid state (Jeppesen et al. 1991; Scheffer et al. 1993). Grazing by duck and geese populations can also threaten the macrophyte dominated, clear water state (Bakker et al. 2016), and make the lake more sensitive to nutrient loading (van Altena et al. 2016). Eventually, without macrophytes, the lake can transition to the alternative turbid state, which is characterized by high phosphorus concentrations, increasing algal blooms and low dissolved oxygen concentrations, which have been considered to have lower ecological value (Carpenter et al. 1999).

There are two classic examples of regime shifts in marine systems: kelp forest/urchin barrens and coral dominated/macrophyte dominated reefs. The first involves shifts between kelp forests and urchin barrens (Estes and Palmisano 1974; Filbee-Dexter and Scheibling 2014). Kelp forest ecosystems in temperate coastal waters are dependent on otters. Otters prey on sea urchins, which in turn graze on kelp. When otters disappear from the system, due to overfishing, disease or predation, urchins graze down the kelp, which causes a regime shift to urchin barrens. The second example was documented on Jamaican coral reefs, where healthy reefs shifted from coral dominated to fleshy macrophyte dominated (Hughes 1994). The proximal cause of this shift was the die-off of the sea urchin, *Diadema antillarum*. However, other herbivorous fish had already been removed by overfishing so when the urchin disappeared, algae overgrew the coral reef. These are classic examples because the shift between states was fairly rapid and moved from a state that is more desirable (to humans) to a more degraded state. There are also well-known shifts in fisheries in the marine environment which are due to natural climatic cycles and are not necessarily anthropogenically induced. Examples include the shift between anchovy dominance and sardine dominance in the Pacific (Chavez et al. 2003) and between

herring dominance and anchovy dominance in the Atlantic (Southward et al. 1988).

Alternate stable states have also been suggested in other aquatic habitats. In the southwestern United States, wide, slow-flowing, riverine wetlands (ciénegas) were common until the late nineteenth and early twentieth centuries when climatic variation and increased cattle grazing altered vegetation and disturbed soils, thereby increasing erosion and incision, which drained the wetland, resulting in further vegetation loss (Heffernan 2008). This resulted in a stable state of deeply incised channels (arroyos). In the Florida Everglades, increases in nutrients caused the historic state of sawgrass marshes and wet prairies to switch to a state dominated by cattails (Gunderson 2001). Recent data from the Prairie Pothole Region of North America suggests that changes in hydrologic or climatic variables may shift a non-floodplain wetland into an alternate state (Mushet et al. 2018). Alberti and Marzluff (2004) suggested two potential alternative stable states in urban areas: an urban attractor with little natural capital (Table 1) and little ecological connectivity and a natural attractor which provides more ecosystem services (Table 1) but fewer human-engineered services. Streams in urban areas reflect these regimes, with urban streams being highly modified with a predictably degraded biotic state (“urban stream syndrome”; Walsh et al. 2005).

Regime shifts may also be functional, as was seen in anoxic mine drainage lakes impacted by increasing groundwater influx, where sediments shifted from iron-reduction to sulfate-reduction (Blodau and Knorr 2006). There may be also regime shifts that are not necessarily rapid or abrupt. Estuaries respond to eutrophication similarly to lakes, shifting from a benthic dominated system, with rooted macrophytes and good water quality, to a pelagic dominated system characterized by high phytoplankton biomass, high turbidity and hypoxia (Viaroli et al. 2008; Krause-Jensen et al. 2012). However, response to eutrophication is often gradual, likely due in part to dilution of nutrient inputs due to estuary flushing from tidal action and riverine flow. Similar to other regime shifts, these systems rarely recover to their previous, historical undegraded condition (Duarte et al. 2009).

This paper explores how resilience concepts have been identified and interpreted in a variety of aquatic habitats as well as their associated socioecological systems to help address its application to restoration and management.

## Materials and methods

Using Google Scholar and Google, we assembled literature – primarily peer-reviewed articles but also some book chapters, using the following keywords: ‘resilience’, ‘recovery’, ‘resistance’, ‘stable states’, ‘alternative states’, ‘restoration’,

'hysteresis', 'thresholds', and 'trophic cascades', in combination with 'lake', 'stream', 'river', 'coast', 'estuary', 'estuarine', 'wetland', and 'aquatic'. We also searched for 'microbial community resilience' and 'restoration.' We selected articles that focused on ecological processes and biological communities and excluded papers examining infrastructure resilience. We also focused on resilience concepts associated with aquatic systems and specifically excluded terrestrial systems. Concepts and phrases as well as cited papers from the selected articles were used to identify additional sources. We later searched for 'socio-ecological resilience', 'ecosystem services', and 'management.' These latter articles were screened to identify those that directly applied to the ecological systems identified in the first round of source assembly and assessment. We then included articles that were not focused specifically on resilience but helped to provide examples of the concepts highlighted in the resilience papers. The search was not temporally bounded initially, but later searches were constrained to between 2015 and 2019. Later searches focused on 'early warning indicators', 'biodiversity and resilience', and 'metapopulations and resilience.' We grouped sources by common themes, identified commonalities across aquatic systems, and summarized them from a resilience perspective. Methods for regime shift detection were highlighted. Socioecological resilience as an expansion of ecological resilience was described. We then compiled the factors affecting resilience of ecological and socioecological systems across aquatic systems and examined how resilience themes and concepts were applied to restoration and management.

## Results and discussion

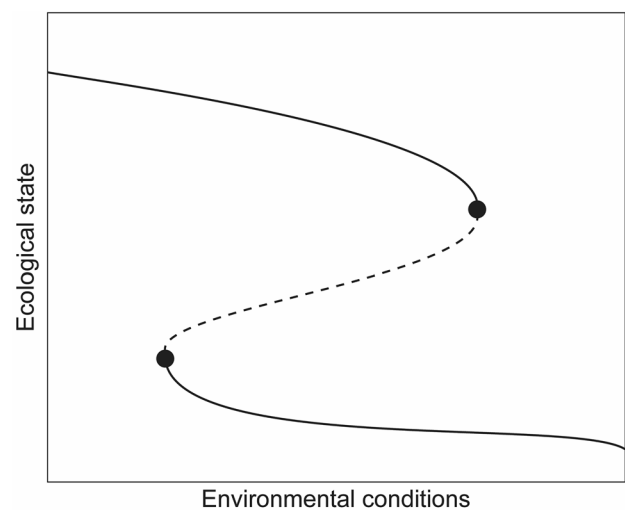
### Detection of regime shifts

Regime shifts are generally not detected until an ecosystem has shifted into an undesirable state. Therefore, there is a need to understand how and why these shifts occur, and whether a system is approaching an ecological threshold or tipping point (Table 1) in order to anticipate and address impacts before a shift in state. Occurrence of shifts in ecological communities have been detected using a variety of statistical techniques (Anderson et al. 2009), including Principal Components Analysis (PCA), clustering and F-tests (Weijerman et al. 2005; Cloern et al. 2010; Spenser et al. 2010; Chaalali et al. 2013). Weijerman et al. (2005) used PCA and chronological cluster analysis with invertebrate, fish, bird, marine mammal and climate data to detect two regime shifts between 1970 and 2002 in the North and Wadden Sea. PCA has also been combined with a regime shift detection algorithm (Radionov 2004) to summarize ecological data and detect regime shifts (Cloern et al. 2010; Spenser

et al. 2010). Cloern et al. (2010) summarized shrimp, crab and fish catches in San Francisco Bay, detecting a regime shift that was related to climate changes. Spenser et al. (2010) summarized six different biological communities in seven areas around the United Kingdom and Ireland that were interpreted as a temporal trend rather than a true regime shift. Other techniques have also been used that look for specific changes in a single aspect of the ecosystem. Rebstock (2002) used locally weighted regression after removal of seasonal trends to look for shifts in California copepod populations. Anderson et al. (2009) used the maximum of F (Quandt 1958) to find a change point in bottom dissolved oxygen in the Danish straits.

There are a few issues with the use of statistical techniques to detect shifts. First, as the numbers of potential shifts increase, detection becomes progressively more difficult (Anderson et al. 2009). In addition, Petraitis and Hoffman (2010) demonstrated that alternative states may not be associated with non-linear dynamics or thresholds, so not all alternate regimes may be detected. Although these techniques may be useful to detect a shift after it has occurred, they do not allow prediction of a regime shift. They also do not identify the underlying cause of the shift, although some of the causes may be inferred by corresponding shifts in climate or stressors.

Early warning indicators (Table 1) have been developed to indicate if a system is close to a threshold, so that an ecological shift might be prevented. These early warning indicators are based on mathematical predictions of how a system responds when multiple alternative states are possible. As a system approaches a transition point (Fig. 3),



**Fig. 3** Conceptual model showing the transition between two states. The solid line indicates a stable state, while the dotted line shows an unstable transition area. The solid dots show thresholds where there can be a sudden transition to a new ecological state

it recovers more and more slowly to small perturbations (critical slowing down). Alternately, as the transition point gets very close, the system may ‘flicker’, briefly visiting each state (Scheffer et al. 2015). A variety of methods to measure autocorrelation and spectral properties and metrics to quantify variability and skewness have been developed and tested using simulated data (Dakos et al. 2012). Detection of potential shifts is more likely using a combination of approaches and metrics (Dakos et al. 2012; Burthe et al. 2016; Gsell et al. 2016). When these indicators were tested using real-world data from lakes and the North Sea, these indicators did not show good agreement with one another and were not particularly predictive (Burthe et al. 2016; Gsell et al. 2016). More recently, Butitta et al. (2017) suggested that spatial rather than temporal autocorrelation early warning indicators may be an effective approach to detect regime shifts. Similarly, Clements et al. (2017) suggested that using biological trait data such as body size along with abundance data to calculate early warning indicators will allow better prediction of regime shifts.

In order to detect or predict regime shifts, appropriate data are needed (Collie et al. 2004; Dakos et al. 2012, 2015; Clements et al. 2017, 2019) along with knowledge of the system and underlying mechanisms which may cause a regime shift (Hewitt and Thrush 2010; Gsell et al. 2016). Both Collie et al. (2004) and Clements et al. (2019) pointed out that biological data have a low signal to noise ratio, which may mask the underlying shift. Monitoring data may not have enough spatial or temporal resolution to allow use of early warning indicators. Clements et al. (2019) suggested that using early warning indicators may work better as early recovery indicators in collapsed systems that are being restored, as these may have more data collected to assess management effectiveness. However, even with good data the effectiveness of early warning indicators may be adversely impacted by extreme events, strong external drivers such as climate cycles, or high environmental stochasticity (Dakos et al. 2015). In addition, as ecosystems become more complex, early warning signals become less predictive (Boerlijst et al. 2013).

Anticipating and preventing unwanted regime shifts in a socioecological system (next section) may be even more difficult than in ecological systems alone as it requires an understanding of the complex processes that support or undermine the resilience and the socio-economic drivers and the governance systems that shape resources (Hughes et al. 2005). Additionally, the complex interactions in a socioecological system make it challenging to isolate a system property or principle (such as diversity) and establish its connection to the resilience of an ecosystem service (Biggs et al. 2012).

## Socioecological resilience

Although early theoretical work on resilience focused solely on ecological systems, it soon became apparent that human interactions with these systems must be considered as they both effect environmental change and suffer impacts from that change. As with ecological resilience generally, socioecological resilience (Table 1) refers to the coupled system’s ability to retain similar structure, function and feedback mechanisms (Walker et al. 2004). Integrated socioecological systems can behave differently than their separate parts, therefore human and ecosystem functions need to be considered together to understand and manage for system resilience (Alberti and Marzluff 2004). An important aspect of socioecological resilience is panarchy (Holling 2001, Table 1), which considers the importance of multiple scales and the adaptive nature of social and ecological systems. Because of this it is important to define both the temporal and spatial scale being assessed or managed (Carpenter et al. 2001; Hughes et al. 2005).

A classic example of socioecological resilience was documented in Lake Mendota, Wisconsin (Carpenter et al. 2001). Development around the lake began at the turn of the century. After World War II, agriculture and urbanization growth led to increased lake enrichment, causing a discernable decrease in water quality. It took a decade for the social system to recognize the impacts of the degraded water quality and for the necessary stakeholders to divert sewage from the lake. This only resulted in marginal improvements in water quality due to intensification of nonpoint inputs (agriculture and urbanization). Attempts to decrease runoff from the more steeply sloped areas of the watershed resulted in little improvement due to the lack of farmer buy-in and participation. Stocking the lake with piscivorous fish to decrease zooplankton grazers initially increased water clarity, but increased fishing pressure diminished the effectiveness of biological control and heavy rains caused increased erosion from cleared construction sites, negating previous gains in water clarity. Finally, in the late 1990s managers and university scientists devised a plan to improve lake clarity by incorporating incentives for farmers to control erosion, enforcement of erosion control at construction sites, as well as purchase of riparian easements and wetlands. Only by incorporating social incentives were management actions able to promote continuous improvement. This case study highlights two points. First, degradation can occur over a long period (in this case 50 years) due to activity in the social system, but management actions were only taken when lake conditions become sufficiently degraded as to impact humans. Second, once degraded, the ecological system may require continuous management actions to maintain the resilience of the clear water state. In recent years, record rains and an invasive waterflea that preys on important

plankton grazers (*Daphnia* spp.) that maintain water clarity, have threatened resiliency (Ness 2017). In contrast, another invasive, the zebra mussel, may increase water clarity. The story of this classic lake is one of continual change in both the social and ecological components of the system, suggesting the need for continual assessment of the ecological system and adaptation in the social system.

When ecosystems are altered by stressors, these changes can also increase the vulnerability of people and ecosystems to further change (Carpenter et al. 2006). These changes can be rapid or slow and can be either predictable or unpredictable. A slow loss in resilience can set the stage for even larger changes when an ecosystem crosses a threshold and experiences a regime shift, thereby causing substantial changes in ecosystem services and human well-being (Folke et al. 2004; Carpenter et al. 2006). These stressors are sometimes referred to as “slow-onset hazards” or chronic disturbances because of their longer-time scales for impact on the social and/or ecological systems (Cutter et al. 2008; Merrill et al. 2018). Although these slow-onset hazards can be difficult to identify and manage because of their longer time spans for impacts, this fact provides increased possibility to allow for social adaptation and possible mitigation of the hazards (Cutter et al. 2008). The response of these systems will depend upon the ecological and social context (Duh et al. 2008), and robust social networks will promote resiliency (Gunderson et al. 2006). These societal pressures challenge the resiliency of watersheds and their ability to provide benefits and ecosystem services to society (Merrill et al. 2018).

Socioecological resilience requires definition of the state being considered (Carpenter et al. 2001). In the example above, this was the clear water state. This desired state can be defined and quantified using the concept of ecosystem services (Millennium Ecosystem Assessment 2005). Ecosystem services are the benefits provided to humans from nature (Costanza et al. 1997). They provide a way to understand the relationships among the social and ecological systems (Lin et al. 2019). Because it is not possible to increase the resilience of all ecosystem services at one time, there are necessary trade-offs between services and across scales (Robards et al. 2011; Biggs et al. 2012; Birge et al. 2016). These trade-offs are necessary because ecosystem services rely on the natural capital (Guerry et al. 2015; Woodhead et al. 2018) provided by ecosystems. Researchers have worked to quantify this by linking biodiversity to ecosystem function (Durance et al. 2016; Oliver et al. 2016). Economic methods have also been used to quantify both use and non-use values of ecosystems. However, there are issues with using economic models. First, not all services can be easily measured or quantified (Guerry et al. 2015; Diaz et al. 2018; Woodhead et al. 2018). Second, natural resources are often inelastic to price (i.e., higher price will not reduce demand), which complicates economic valuation (Farley and

Voinov 2016). Finally, the value of ecosystem services is context-specific (Cote and Nightingale 2012; Pearson et al. 2015; Diaz et al. 2018; Sattler et al. 2018; Woodhead et al. 2018). What is valued depends upon the cultural and social context of the system, as well as competing interests and the balance of power. Scale will also be important – what enhances ecosystem services at one scale or for one set of stakeholders may reduce overall system resilience. Recent work on ecosystem services recognizes that natural capital is the foundation of all ecosystem services, and that incorporation of cultural beliefs and concerns is needed to increase resilience of the overall system.

### Factors affecting the resilience of aquatic systems

Because we do not yet have methods to prevent ecological shifts, we need to be able to understand what increases or decreases system resilience (Table 2). In general, stressors that adversely impact communities also decrease resilience. Although the system may be initially resilient, eventually resilience may be degraded to the point where ecosystem condition is also diminished. Resilience is also reduced by lack of equity in the socioecological system. Power imbalances tend to promote use of the resource by certain actors without consideration of the needs of other stakeholders or the overall system. Resilience is maintained or enhanced by connectivity, habitat heterogeneity, functional redundancy (Table 1) and diversity. These factors allow the system to compensate for stress and/or promote recovery after adverse impacts. Strong linkages between the social and ecological system also enhance resilience. Disturbance and life history characteristics may increase or decrease resilience depending upon environmental conditions and scale. In addition, the resilience of a system depends upon its spatial or temporal scale. Understanding interactions at multiple scales will be necessary to promote resilience.

### Factors decreasing resilience

Resilience can be reduced by increasing stressor loads. A common stressor in aquatic systems is nutrient overenrichment. Generally, high nutrient loading shifts ecosystems from benthic dominated to pelagic dominated production. Classically, nutrient (phosphorus) inputs to lakes can cause lakes to shift from a clear into a turbid state. These shifts can take place over the course of months or years and can oscillate between stable states frequently (Scheffer and Jeppesen 2007). During this period, excess phosphorus can be bound to insoluble iron compounds in the sediments (Carpenter 2003). Although the exact concentrations needed to cause this shift are unknown, thresholds for total phosphorus concentrations in the water column have been speculated (Jeppesen et al. 1991; Wang et al. 2014). Once in the turbid

**Table 2** Factors affecting resilience

Direction of Influence	Factor	References
Decreasing	Increasing stressor loads (e.g., nutrients and contaminants)	Jeppesen et al. (1991), Søndergaard et al. (1992), Peterson et al. (1998), Carpenter et al. (1999), Carpenter (2003), Søndergaard et al. (2003), Munkes (2005), Troell et al. (2005), Howarth and Marino (2006), Scheffer and Jeppesen (2007), Viaroli et al. (2008), Wang et al. (2014), Feio et al. (2015), Johnston et al. (2015), Zeglin (2015), Bush et al. (2017), Moksnes et al. (2018), Moore and Cuker (2018), Watson et al. (2018)
	Urbanization	Roy et al. (2003), Small and Nicholls (2003), Morgan and Cushman (2005), Griffiths et al. (2014), Uden et al. (2014), McCauley et al. (2015)
	Overharvesting	Jackson et al. (2001), Savenkoff et al. (2007), Lotze and Worm (2009), Lotze et al. (2011), Hamilton and Caselle (2015), Roth et al. (2015), Bozek et al. (2016)
	Climatic changes	Scavia et al. (2002), Tompkins and Adger (2004), Palumbi et al. (2008), Bottom et al. (2009), Shanley and Albert (2014), Duarte et al. (2015), Farley and Voinov (2016), Pinceel et al. (2018)
	Multiple stressors	Dayton et al. (1998), Estes et al. (1998), Breitberg et al. (2009), Conley et al. (2009), Waycott et al. (2009), Maina et al. (2011), Wernberg et al. (2011), Albins and Hixon (2013), Holdschlag and Ratter (2013), Anthony et al. (2015), Duarte et al. (2015), Kernan (2015), Unsworth et al. (2015), Zhang (2016), Oreska et al. (2017), Orth et al. (2017), Corrales et al. (2018), Ramírez et al. (2018)
	Lack of equity (in the socioecological system)	Ostrom (1999), Rhoads et al. (1999), Scheffer et al. (2000), Hagy et al. (2004), Bottom et al. (2009), Worm et al. (2009), Campbell and Butler (2010), Levin and Möllman (2015), Farley and Voinov (2016), Holdschlag and Ratter (2013), Poff et al. (2016), Berkes (2017)
Increasing	Connectivity	Detenbeck et al. (1992), Fritz and Dodds (2004), Ray (2005), Carpenter et al. (2006), Elliot et al. (2007), Palumbi et al. (2008), Thrush et al. (2009), Lotze et al. (2011), Olds et al. (2012), Beechie et al. (2013), de Juan et al. (2013), McCluney et al. (2014), Uden et al. (2014), Bogan et al. (2015), Castorani et al. (2015), Duarte et al. (2015), Flotemersh et al. (2016), Cohen et al. (2016), Deacon et al. (2018), Terui et al. (2018), Campbell et al. (2019)
	Habitat heterogeneity	Penfound (1952), Pearsons et al. (1992), Seabrook and Townsend (1993), Beck et al. (2001), Mumby et al. (2004), Bisson et al. (2009), Euliss et al. (2004), Cicchetti and Greening (2011), US EPA (2012), Hershkovitz and Gasith (2013), Mushet et al. (2013), Mantyka-Pringle et al. (2014), Massicotte et al. (2015), Chretien and Chapman (2016)
	Functional redundancy	Doak et al. (1998), Peterson et al. (1998), Elmqvist et al. (2003), Carpenter et al. (2006), Nyström (2006), Walker et al. (2006), Allison and Martiny (2008), Levin and Lubchenco (2008), Bottom et al. (2009), Schindler et al. (2010), Carlson and Satterthwaite (2011), Biggs et al. (2012), Hoppe et al. (2017), McWilliam et al. (2018), Angeler et al. (2019)
	Diversity	Petersen et al. (1998), Gunderson (2000), Stachowicz et al. (2002), Elmqvist et al. (2003), Bell et al. (2005), Hughes et al. (2005), Nyström (2006), Palumbi et al. (2008), Thrush et al. (2009), Davies et al. (2011), Elliott and Whitfield (2011), Lotze et al. (2011), Magurran and Henderson (2012), Oliver et al. (2015), Strong et al. (2015), Woodward et al. (2015), Angler and Allen (2016), Angeler et al. (2016), Dee et al. (2016), Duffy et al. (2016), Pires et al. (2018), Sundstrom et al. (2018), Thornhill et al. (2018), Wernberg et al. (2018)
	Strong linkages between the social and ecological systems	Rhoads et al. (1999), Carpenter et al. (2006), Arnold et al. (2014), McPhearson et al. (2014), Restall and Conrad (2015), Folke et al. (2016), Abson et al. (2017), Reyers et al. (2018), Ives et al. (2018), von Putten et al. (2018), Wondie (2018)



**Table 2** (continued)

Direction of Influence	Factor	References
Depends upon context	Disturbance	Detenbeck et al. (1992), Peterson et al. (1998), Peterson (2000), Tompkins and Adger (2004), Lepori and Hjerdt (2006), Elliot et al. (2007), Ledger et al. (2012), Duarte et al. (2015), Ellender and Weyl (2015), Fu et al. (2015), Woodward et al. (2015), Chaffin and Gunderson (2016), Diggelen and Montagna (2016), Gunderson et al. (2017), Rehitha et al. (2017), Timpane-Padgham et al. (2017), Haghkerdar et al. (2018), Milner et al. (2018), Rolls et al. (2018)
	Life history characteristics	Pearsons et al. (1992), Bisson et al. (2009), Tisseuil et al. (2012), Ibrahim et al. (2014), Ryan et al. (2014), Chester et al. (2015), Clarke et al. (2015), Kernan (2015), Cullen-Unsworth and Unsworth (2016), Leigh et al. (2016), Sievert et al. (2016), Aspin et al. (2018), Rolls et al. (2018)
	Scalar issues	Estes et al. (1998), Scavia et al. (2002), Scheffer and Carpenter (2003), Carpenter et al. (2006), Simenstad et al. (2006), de Yong et al. (2008), Powell et al. (2008), Bottom et al. (2009), Lundquist et al. (2010), Elliott and Whitfield (2011), Lotze et al. (2011), Casini et al. (2012), Ling et al. (2015), Berkes (2017)

state, even with external phosphorus loading reduced, the lake may be resistant to shifting back to the clear state until the sequestered phosphorus is depleted from the sediment. Additional management techniques may need to be implemented (Carpenter et al. 1999; Søndergaard et al. 2003) because both resuspension and microbial processes are important for mediating the release of sequestered phosphorus into the water column (Søndergaard et al. 1992). Microbial communities may also mediate oxic and anoxic regimes in lakes, with cyanobacteria dominating in oxic conditions, and sulfur bacteria dominating in anoxic conditions (Bush et al. 2017). In estuaries, nitrogen loading is the main nutrient decreasing resilience, although phosphorus can also cause deleterious impacts, especially in lower salinity waters (Howarth and Marino 2006; Zedler 2017). As in lakes, nutrient inputs cause estuaries to shift from a state allowing for growth of seagrass and macrophytes to a turbid state dominated by phytoplankton and algal mats (Munkes 2005; Troell et al. 2005; Viaroli et al. 2008). Once in the turbid state, positive feedbacks act to maintain this state. Decreased circulation, sediment and organic matter accumulation, resuspension, release of nutrients from the sediments, and anoxic and sulfidic conditions act to keep lagoons and estuaries in their degraded state (Munkes 2005; Troell et al. 2005; Viaroli et al. 2008; Moore and Coker 2018). Conditions that promote algal mat formation tend to decrease the probability of recovery (Moksnes et al. 2018; Watson et al. 2018). Beyond the impacts of nutrient pollution, other anthropogenic chemicals also decrease community diversity, which has been shown to decrease resilience (Peterson et al. 1998). Feio et al. (2015) found that mining effluent resulted in functionally homogeneous stream invertebrate communities that responded similarly to temperature

and rainfall extremes, resulting in decreased resilience to other stressors. However, contaminant impacts seem to have fewer and less widespread impacts than nutrient overenrichment. For example, in marine systems, contaminant effects were often only seen at the individual level. When multiple functions or taxa were included, effects were often not seen, perhaps due to interactions among components of the larger system (Johnston et al. 2015). Similarly, while Zeglin (2015) found widespread and significant impacts of metals on microbial diversity, this response may be mediated by changes in environmental variables such as organic matter quality or quantity and hydrology.

A more generalized stressor is urbanization and associated land use changes. Increased human population growth and associated urbanization along with increased agricultural production and energy extraction have led to increased impervious cover, runoff, non-point source pollution and habitat fragmentation. With increasing impervious surface in the watershed, stream and river hydrology is altered, increasing sediment and contaminant loads, which causes adverse impacts on nearby aquatic systems. This is especially true in the coastal zone where over 50% of the world's cities and over 38% of the world's human population live (Small and Nicholls 2003). Urbanization has been shown to decrease the diversity of stream macroinvertebrates (Roy et al. 2003), and fish (Morgan and Cushman 2005). It can also cause aquatic populations to become more synchronized, and vulnerable to collapse. Pacific salmon populations along the US west coast showed decreasing behavioral and life history diversity as their watersheds became more developed with a greater number of dams (Griffiths et al. 2014). Urbanization can adversely impact wetlands through ditching, draining, or filling wetlands, which may ultimately

lead to wetland loss. Similarly, deepening or consolidating wetlands reduces their suitability as habitat for amphibians and breeding birds (McCauley et al. 2015). Hydrological modifications may decrease spatial resilience by changing the distance between wetlands, which can negatively affect certain native amphibians with limited migration ability while favoring larger non-native predators that can migrate over much longer distances (Uden et al. 2014).

Overharvest of fish and apex predators has been well-documented as a cause of decreased resilience. Historically abundant marine mammals, bird and commercially exploited fish and invertebrate species have declined 75% to 95% from historic baselines (Lotze and Worm 2009), resulting in large ecosystem shifts (Lotze et al. 2011). Overfishing of piscivores caused an ecosystem shift to a community with fewer demersal fish and more forage fish (Savenkoff et al. 2007). Overfishing can also cause predatory fish to shift to smaller size classes. For example, larger predatory fish were needed to keep sea urchin numbers low enough to favor kelp forest persistence (Hamilton and Caselle 2015). Overhunting of otters for the fur trade eventually led to the destruction of kelp forests and their replacement by urchin barrens (Lotze et al. 2011). Coral reefs have also been negatively impacted due to overfishing. In the Caribbean this was due to overfishing of herbivorous fish, but in the Great Barrier Reef, overfishing may have resulted in a release of crown-of-thorns starfish, which eat corals (Jackson et al. 2001). Overfishing of parrotfish causes coral decline, but a reduction in fishing pressure may increase coral resilience (Bozec et al. 2016). In an upwelling area of Costa Rica, overfishing may also allow the overgrowth of colonial ascidians (Roth et al. 2015). The widespread decline in seagrass in tropical areas may have been due in part to overfishing of sea turtles (Jackson et al. 2001).

Climatic changes can cause a cascade of changes (Scavia et al. 2002) that adversely impact aquatic habitats by altering the landscape, decreasing ecosystem resilience. These changes may be self-reinforcing, resulting in systems being pushed well beyond expected ecological thresholds (Farley and Voinov 2016). Changes in wind and rainfall patterns can alter hydrology—leading to droughts or increased flashiness. More frequent floods may scour eggs from spawning substrates (Shanley and Albert 2014), which can decrease population viability. Changing precipitation patterns will alter water and sediment delivery to coastal waters making nutrient loading more extreme and variable (Scavia et al. 2002). Extreme events such as droughts and floods are expected to add additional stress to the socioecological system (Tompkins and Adger 2004). Predicted temperature increases will impact species metabolism and species distribution patterns. Freshwater zooplankton in temporary ponds may be particularly vulnerable, as climate change may decrease available habitat while also decreasing hatching success (Pincheel et al.

2018). In addition, climate change may alter the underlying physical forces driving existing climate cycles (Palumbi et al. 2008). Different ecosystems may be expected to respond differently. Marshes may drown due to sea level rise if they are unable to migrate into the upland, causing ecological shifts from marsh to open water. In estuaries, changes in freshwater inputs will change salinity and stratification as well as alter flushing and exchange rates. The interaction between anthropogenic stress and natural climate cycles can lead to unforeseen ecological impacts, especially in marine fisheries, as favorable climate conditions may lead to high natural stock levels which may temporarily mask underlying degradation in the underlying system. An example is the collapse of the sardine industry in Monterey Bay due to high fishing pressure followed by a switch in the Pacific Decadal Oscillation to a cool period, which did not favor sardine population growth (Palumbi et al. 2008). Another is the collapse of the coho salmon, where hatchery stocks and good offshore conditions masked issues in recruitment for an extended period (Bottom et al. 2009). Finally, climate change impacts the ecological baselines of these systems which will affect both restoration and preservation efforts (Duarte et al. 2015).

While a single stressor may be the dominant cause of adverse impacts, most systems are impacted by multiple stressors. For example, excess loading from agricultural and urban sources may require phosphorus and nitrogen to be co-managed to control eutrophication in marine and freshwater systems (Conley et al. 2009). Similarly, overfishing and eutrophication can have interacting effects and would be best managed such that both stressors are considered (Breitberg et al. 2009; Zhang 2016), especially in the context of warming coastal waters (Ramírez et al. 2018). There is evidence that coral reefs that are stressed by eutrophication and sedimentation may be more vulnerable to climate change impacts (Maina et al. 2011). In addition to eutrophication and sedimentation, coral reefs can be affected by climate change related impacts such as storms, bleaching and acidification as well as overfishing, physical damage, and pollution (Anthony et al. 2015). Invasive species combined with other stressors may decrease resilience. The Pacific red lionfish, *Pterois volitans*, is a voracious predator on coral grazers (Albins and Hixon 2013), which in addition to overfishing and coastal development (Holdschlag and Ratter 2013) greatly reduces coral reef resilience. In the Mediterranean, it was predicted that climate change and invasive species impacts may overwhelm positive management actions designed to decrease fishing pressure and rebuild fishing stocks (Corrales et al. 2018). Seagrass can be adversely impacted by physical damage, invasive species, climate change, eutrophication and sedimentation (Waycott et al. 2009; Unsworth et al. 2015). Dredging of seagrass beds reduced shoot density (Oreska et al. 2017), which made

seagrass less able to withstand storm events and moderate declines in water quality (Orth et al. 2017). Interacting stressors can alter expected response to a single stressor. In the classic example of kelp forests shifting into an alternative state, overfishing causes a trophic cascade that results in an alternative urchin barren state. However, in southern California, kelp forests survived even after the dominant grazers were removed due to environmental changes mediated by oceanographic cycles (Dayton et al. 1998). In Australia, urchin barrens developed due to climate shifts and associated warming waters rather than a trophic cascade after urchin removal (Wernberg et al. 2011). Another example of multiple stressor impact was seen in Alaska (Estes et al. 1998), where diminished forage fish availability, perhaps due to fishing and temperature changes, has led to declines in marine mammals. Killer whales then began preying on sea otters, which led to predictable declines in kelp forests. The impact of multiple stressors may affect the potential for restoration; once the major known stressor has been reduced or eliminated, other stressors may retard recovery (Duarte et al. 2015). While seagrass recovery has been achieved using nutrient reduction, other restoration efforts have combined nutrient reduction with altered fishing practices and physical interventions to alter hydrology (Waycott et al. 2009).

A final factor that may decrease resilience in the ecological system is a lack of equity in the socioecological system. Because ecological resources and their associated social systems are common-pool resources where everyone theoretically has equal access, individual users can impact the resource to the detriment of others (Ostrom 1999; Berkes 2017). Similarly, market forces may promote actions that reduce system resilience (Farley and Voinov 2016). For example, costs due to alternative energy patents may promote continued use of coal. One set of users may benefit from actions that eventually adversely impact the ecological system, (e.g., nutrient addition from agricultural lands to lakes) while the costs of those uses are borne by another group within the social system (Scheffer et al. 2000). The strength of the cultural or economic linkages to the ecological system and sense of ownership will affect the willingness of people to support management actions to promote resilience (Bottom et al. 2009; Campbell and Butler 2010). The Susquehanna River contributes most of the nitrogen loading to the mainstem of Chesapeake Bay (Hagy et al. 2004), much of which originates from the watersheds in Pennsylvania, where many of the residents have little or no connection to the bay. In addition, difference in values among stakeholders may result in decisions that do not enhance resilience of the entire system (Rhoads et al. 1999; Poff et al. 2016) and the monetary cost to avoid adverse impacts may be considered too high to deal with a hypothetical future issue (Levin and Möllman 2015). Actions to control pressures on the ecological systems may also have significant adverse impacts

on the resilience of the social system. Attempts to reduce overfishing often result in the loss of fishing jobs (Worm et al. 2009), which provokes predictable political backlash against these management measures. Finally, the portions of the social system that benefit from exploiting the system are often more powerful than those trying to protect it (Scheffer et al. 2000; Holdschlag and Ratter 2013). Business and agricultural interests may have more political clout, due to their economic contributions, than environmental interests.

### Factors increasing resilience

Many studies emphasized the importance of connectivity to resilience of aquatic ecosystems (Carpenter et al. 2006; Elliott et al. 2007; Thrush et al. 2009; McCluney et al. 2014; Flotemersch et al. 2016). Connectivity can positively impact resiliency by increasing aquatic population dispersal and recruitment success (Carpenter et al. 2006) which can facilitate ecosystem recovery (Ray 2005; Elliott et al. 2007; Palumbi et al. 2008; Thrush et al. 2009; Lotze et al. 2011; de Juan et al. 2013; Duarte et al. 2015). Stream invertebrate communities were more likely to recover from extreme drought in well-connected streams, with short-lived dispersers replacing longer-lived, weaker dispersers (Bogan et al. 2015). In estuaries, connectivity with the regional species pool can help to support local benthic communities (de Juan et al. 2013), while more connected patches of kelp (via passively drifting spores) had higher probability of existence and lower probability of extinction (Castorani et al. 2015). Connectivity also allows access to multiple habitats and refugia. In streams, macroinvertebrate colonization was related to distance from upstream refugia (Fritz and Dodds 2004), while salmonid populations were able to expand into lakes when hydraulic conductivity was high (Campbell et al. 2019). In contrast Detenbeck et al. (1992) noted that the resilience of stream fish communities was reduced by migration barriers. Streams with good connections between ground water and surface water may allow maintenance of cooler thermal refugia for salmon, improving their resilience (Beechie et al. 2013). In wetlands, man-made ponds may help maintain wetland amphibian (Uden et al. 2014) and pond insect populations (Deacon et al. 2018) by improving connectivity across the landscape. In estuaries, connectivity between reefs and seagrasses can increase the diversity of organisms in the reef system (McCleod et al. 2019). Similarly, good connectivity between mangroves and protected areas enhanced the biomass of herbivorous fish on the reefs, enhancing resilience (Olds et al. 2012). However, variation in connectivity may also be important in maintaining resilience. For example, although watershed area is thought to be a surrogate for metapopulation stability, Terui et al. (2018) showed that amount of branching in river networks was more important than size, assuming that among

branch heterogeneity was high. Similarly, varying connectivity in isolated wetlands may help to maintain unique biological communities (Cohen et al. 2016). Resilience of the watershed is enhanced by spatial and temporal connectivity among its individual components (Flotemersh et al. 2016) while stream resilience is determined by connectivity across scales (reach, sub-basin and basin) due to impacts and feedbacks between scales (McCluney et al. 2014).

Habitat heterogeneity (diversity) can help to maintain or improve resilience. This improvement can be due to a variety of mechanisms (Bisson et al. 2009), including the use of multiple habitats by taxa for different purposes, access to neighboring high-quality habitats, redundancy of habitats (i.e., insurance effect) as well as support for metapopulations. Habitat diversity may also act to promote response diversity (Table 1), directly via buffering and ‘insurance’ effect of environmental heterogeneity on physical disturbance, or indirectly via maintenance of an environmental template that fosters functional diversity (e.g., life history diversity, genetic diversity within species; Table 1). In streams, habitat complexity can provide refugia to both invertebrates and fish (Pearsons et al. 1992; Seabrook and Townsend 1993; Hershkovitz and Gasith 2013) as well as improve the resilience of native communities to invasive species (Chretien and Chapman 2016). Riparian habitat restoration has been shown to improve resilience in streams (Mantyka-Pringle et al. 2014) and large-scale habitat diversity was found to improve the resiliency of northern leopard frog populations in wetlands (Mushet et al. 2013). Wetlands often have within-system heterogeneity due to hydrological differences in flooding depth, duration, and timing (Penfound 1952; Euliss et al. 2004) which imparts resilience. Watershed habitat diversity affects habitat quality and species population which enhances watershed resilience (US EPA 2012). In estuaries, many different habitats, especially marshes, mangroves and seagrass provide needed nursery and juvenile habitat (Beck et al. 2001; Mumby et al. 2004) while Massicotte et al. (2015) determined that species richness of coastal fish populations was related to the spatial heterogeneity of water column characteristics. Habitat diversity is often needed to maintain valued faunal groups (Cicchetti and Greening 2011).

Functional redundancy also helps to maintain resilience (Peterson et al. 1998; Elmqvist et al. 2003; Nyström 2006; Walker et al. 2006; Levin and Lubchenco 2008; Biggs et al. 2012; Angeler et al. 2019). Functional redundancy is sometimes referred to as response diversity, but they may be more accurately viewed as related and interconnected concepts. Coral grazers encompass species that graze intensively and locally such as sea urchins as well as those that have wider ranges and graze intermittently like sea turtles (Elmqvist et al. 2003). Thus, if one of these taxa are eliminated, the other coral grazer will still be able to fill the grazer

role (functional redundancy), with the different scales of response indicating response diversity. A lack of functional redundancy has been shown to make corals less resilient and more susceptible to collapse (McWilliam et al. 2018). Functional redundancy in subarctic phytoplankton communities appears to provide resilience to ocean acidification (Hoppe et al. 2017). West coast salmonid stocks have multiple distinct populations (functional redundancy), with different life histories and behaviors (Bottom et al. 2009; Schindler et al. 2010; Carlson and Satterthwaite 2011). This variation (response diversity) causes the individual stocks to respond asynchronously, reducing the variation in the overall stock, and spreading the risk of exposure to stressors across both space and time. A similar decrease in variance can also occur within individual taxa, and has been referred to as the portfolio effect, and has been seen in both relatively pristine habitats (Schindler et al. 2010) and heavily modified river systems (Carlson and Satterthwaite 2011). The portfolio effect is also seen in microbial communities (Doak et al. 1998; Allison and Martiny 2008). The overall service provided by the community stays the same because the positive responses of some taxa are balanced with negative responses of other taxa, resulting in no alteration in function. Response diversity in ecological systems can impact the resilience of socioecological systems; Carpenter et al. (2006) concluded that the resilience of ecosystem services depends on response diversity as indicated by the diversity of species and functional groups that exist in a system.

Diversity is assumed to enhance resilience because with more species, it is more likely that some of them would be able to functionally compensate for extirpated taxa (Gunderson 2000; Bell et al. 2005; Hughes et al. 2005; Palumbi et al. 2008; Oliver et al. 2015; Pires et al. 2018). Diversity in management and institutions can also enhance diversity by providing opportunities for learning and adaptations (Biggs et al. 2012). Highly diverse marine communities have been shown to be more resilient and resistant to invasion (Stachowicz et al. 2002) while low species diversity in some assemblages increase vulnerability (Elliott and Whitfield 2011). Higher diversity ecosystems are more likely to promote recovery of collapsed fisheries (Palumbi et al. 2008) while genetic diversity in kelp provides protection against marine heat waves, allowing kelp forest persistence (Wernberg et al. 2018). Biodiversity has been shown to be related to ecosystem function in both marine and freshwaters, although abiotic factors may drive much of this relationship (Strong et al. 2015; Thornhill et al. 2018). Many authors suggested the need to understand function. Thrush et al. (2009) suggested that protecting keystone species and ecological engineers might provide insurance against regime shifts while Lotze et al. (2011) indicated the importance of understanding life history strategy and food web interactions when predicting potential for recovery. Several authors suggest

that functional diversity (Table 1) is more predictive of ecosystem resilience than species diversity (Elmqvist et al. 2003; Nyström 2006; Thrush et al. 2009). Functional diversity made stream invertebrate communities more resilient to floods and droughts (Woodward et al. 2015), enhanced coral recovery (McCleod et al. 2019), and buffered the impacts of temperature fluctuations to marine fish and fisheries (Dee et al. 2016; Duffy et al. 2016). Several authors suggested that biomass might be a better measure of ecosystem function than abundance (Davies et al. 2011; Magurran and Henderson 2012; Sundstrom et al. 2018). Peterson et al. (1998) first proposed that cross-scale resilience (Table 1) should be considered. Because ecosystems are hierarchical in both space and time, resilience is enhanced when there are species with similar functions at different scales that respond differently to environmental stressors (Angeler et al. 2016) with body size suggested as a proxy for spatial impact (Strong et al. 2015; Angeler and Allen 2016).

The resilience of the overall socioecological system can be enhanced through strong linkages between the social and ecological systems, which Carpenter et al. (2006) suggested could be enhanced via recognition of ecosystem services. Even aquatic systems with reduced resilience and condition may provide important supporting, regulating and cultural services (McPhearson et al. 2014; Wondie 2018) since in urban settings it may not be possible to significantly increase the resilience of the overall ecological system. The resilience of the connected social, economic, institutional and ecological subsystems may be increased through careful urban planning (Arnold et al. 2014) with improved linkages between science and society. In addition, communication needs to be fostered among stakeholders (Rhoads et al. 1999; Reyers et al. 2018) with several authors highlighting the importance of incorporating diverse values, beliefs and cultures (Rhoads et al. 1999; Restall and Conrad 2015; Folke et al. 2016; Reyers et al. 2018). Connectedness to nature is necessary for sustainability (Restall and Conrad 2015; Abson et al. 2017; Ives et al. 2018; van Putten et al. 2018). This connection to nature occurs at both the individual and societal levels (Abson et al. 2017). Connection to nature may involve a 'sense of place,' which can involve both physical access and emotional bonds that help to support conservation and management efforts. Ives et al. (2018) noted that while socioecological systems were more directly influenced by material and experiential connections, cognitive, emotional and philosophical connections are more likely to influence the underlying goals and values driving the system. Finally, Folke et al. (2016) suggested that stewardship is needed to foster sustainability given that social-ecological systems rely upon the biosphere. This stewardship will require not only management of ecosystem services, but also understanding of the social, economic, and cultural context.

### Factors that may increase or decrease resilience depending upon environmental conditions and scale

Some factors that may either increase or decrease the resilience of aquatic systems have been identified (Table 2) including disturbance, life history characteristics and scalar issues. Carpenter et al. (2001) discussed the plasticity of resilience; resilience depends on which system and disturbance is being considered.

While disturbance can have negative effects on systems, it can also help to maintain diversity and allow reorganization of the system, which increases resilience. Floods, disease, pollution, and financial crises can wreak havoc on both ecological and social systems, decreasing resilience (Tompkins and Adger 2004). The timing, magnitude, and frequency of disturbance may be one measure of whether disturbance has positive or negative impacts on diversity. Stream invertebrates and fishes are better able to recover from disturbances occurring prior to spawning (Detenbeck et al. 1992; Milner et al. 2018), and stream biota are most strongly impacted by extreme climate events that are close in time or at an unexpected time (Woodward et al. 2015). Similarly, Fu et al. (2015) showed impacts on wetland plant structural and functional diversity at lowest and highest levels of flood disturbance. Increasing salinity variation was strongly related to decreasing species richness, diversity and evenness in estuarine benthic invertebrate communities (Diggelen and Montagna 2016), while increasing drainage basin hydrologic variability decreased fish diversity (Rolls et al. 2018). More frequent disturbance was shown to adversely impact both stream and estuarine benthic communities (Ledger et al. 2012; Rehitha et al. 2017; Haghkerdar et al. 2018). However, disturbance can also positively impact diversity by diminishing specialization and increasing diversity and flexibility, allowing better responsiveness to varied future stresses (Peterson 2000; Timpane-Padgham et al. 2017). Disturbance can also act to connect ecological scales (Peterson et al. 1998). For example, storms can cause stream flooding that impacts portions of the stream network in different ways; stream macroinvertebrates diversity declines locally but creates a mosaic of habitats enhancing diversity at the landscape scale (Lepori and Hjerdt 2006). Plant diversity has been shown to increase in wetlands, floodplains and riparian areas as flood duration increases (Rolls et al. 2018). Similarly, Ellender and Weyl (2015) suggested that species in unpredictable habitats such as headwater streams may have evolved to be resilient to events. In these environments, the natural disturbance in the system helps increase variation and resilience. Estuaries and coasts are thought to be highly resilient (Elliott et al. 2007), at least in part due to the mosaic of ecological states resulting from the interaction among ecological gradients and stressor gradients (Duarte et al. 2015). Disturbance also allows ecological

systems to reorganize (Gunderson et al. 2017). A drought in the Klamath River Basin in the western US caused conflicts over water allocation to farmers, ranchers, indigenous tribes and endangered species. Over time, litigation, and social conflict led to the development of cross-scale interactions among user groups that allowed new, adaptive governance arrangements in this system (Chaffin and Gunderson 2016).

Life history characteristics may influence whether a community is resilient and may depend upon environmental conditions. In wetlands, amphibians with large clutch sizes, and invertebrates with cold and drought-tolerant eggs or high dispersal ability (e.g., flying stages) are more likely to have persistent populations (Ryan et al. 2014). Life history strategy may also help to explain why species are sensitive to anthropogenic chemical exposure (Ibrahim et al. 2014). Sievert et al. (2016) suggested that knowing which aquatic taxa were intolerant and therefore vulnerable can inform conservation efforts. For example, slow growing seagrass may not be able to recover from boat moorings and anchoring damage, even if eco-friendly moorings are installed (Cullen-Unsworth and Unsworth 2016). Taxa adaptation to droughts or floods may explain taxa persistence or vulnerability. For example, wetlands with highly fluctuating drying regimes tend to be dominated by short-lived clonal plants rather than those sprouted from seeds (Clarke et al. 2015). Droughts promote invertebrates with small body size, aerial dispersion and respiration, generalist feeding, burrowing and desiccation resistance (Aspin et al. 2018). Similarly, invertebrates surviving in intermittent sites were more resistant to drying while those at perennial sites tended to have higher dispersal ability and a longer life span (Leigh et al. 2016). Taxa that prefer fast flow (i.e., EPT) are favored with increasing flow permanence (Rolls et al. 2018). Floods may negatively impact fish species that depend on the timing of the flood in relation to their spawning (Pearsons et al. 1992). Aquatic populations that were resilient under one set of environmental conditions, may become much less so under another set of conditions. Salmon's connection to marine and freshwater habitats made them highly resilient in the past, but now may be a vulnerability as watersheds became more developed (Bisson et al. 2009). Climate change may enhance or decrease the successful expansion of invasive species based on their life history strategy (Kernan 2015). Under increasing temperatures, cold-water fish populations will be expected to decline, while warm-water fish populations will be expected to expand their range (Tisseuil et al. 2012). Dispersal traits and strategies used by invertebrates in intermittent streams may become less effective in a drying climate as effective connectivity decreases (Chester et al. 2015).

Scale mismatches may impact resilience as aquatic ecosystems are controlled and impacted by not only the internal components, but also by the larger systems that encompass

them—and these processes may also vary temporally (Carpenter et al. 2006). Ecological shifts may be seen locally, or regionally. The shift from coral reefs to fleshy algae or kelp forests to urchin barrens is a local phenomenon that has been seen worldwide (de Yong et al. 2008; Ling et al. 2015). Expanding from the local scale may show a mosaic of kelp forests and urchin barrens (Estes et al. 1998). The impact of scale is seen for both stressors and biological response (Scheffer and Carpenter 2003; Elliott and Whitfield 2011). Understanding scale and metapopulation dynamics will be important for ecosystem recovery (Lotze et al. 2011). Lundquist et al. (2010) demonstrated that increased regional dispersal helped the shallow reef community resist disturbance while Casini et al. (2012) showed that trophic shifts in a smaller connected bay may be due to conditions in the Baltic Sea. Several authors noted the impact of spatial shifts in masking environmental impact. Powell et al. (2008) noted that oyster stocks were high but concentrated in lower salinity areas, which made them vulnerable to a later disease outbreak while locational shifts in cod populations caused temporary increases in catch per unit effort which masked an actual decline that led to a stock collapse in the 1990s (deYong et al. 2008). Actions or impacts at one scale can result in cascading, unpredicted or unintended impacts at another scale for both the ecological and social systems. Estuaries are impacted by stressors and forcing factors outside of the immediate system (Elliott and Whitfield 2011) so system-wide constraints in the landscape and larger oceanic systems need to be considered in assessing system resilience (Simenstad et al. 2006). Freshwater requirements and urbanization impacts need be considered on the land side. On the ocean side, rising seas will alter hydrodynamics as well as nutrient and sediment transport (Scavia et al. 2002). Pacific salmon are affected by broad-scale oceanic and climatic cycles that have differing impacts on the oceans and freshwater streams which impacts population size and persistence. In addition, the salmon resource is managed by multiple jurisdictions at the national, regional, state and local scales, which can sometimes result in conflicting or interacting impacts (Bottom et al. 2009). The socio-ecological system may also be impacted by factors outside the immediate system; for example, the Chilean sea urchin industry is driven by the Asian sushi market (Berkes 2017).

## Restoration

We often do not recognize when a system is transitioning into a new state or realize that the system is losing resilience until there is significant degradation of the system. However, once this has occurred there is often a desire to restore the system back to or towards a desired state. These restoration efforts may provide some insights into system resilience.

Unfortunately, it can be difficult to determine recovery. There are often no accepted criteria used to define restoration success (Elliott et al. 2007, 2016; Duarte et al. 2015) so it is necessary to set clear restoration goals and indicators of success (Duarte et al. 2015; Zhao et al. 2016; White and Kaplan 2017). Although restoration aims to reestablish the structure and function of the naturally occurring ecosystem, existing anthropogenic alterations may make this goal impossible to achieve (Brown et al. 2018; Sinclair et al. 2018). Thus, it may be more tractable to focus on restoring functions and processes, desirable ecosystem services, or ecosystem integrity and resilience (Alexander et al. 2016; Krievins et al. 2018). Historical data including information on past disturbance regimes, historical trajectory and regional processes may give insights into what may be possible for a given restoration effort (Pearson et al. 2015; Brown et al. 2018; Knudson et al. 2018; Lin et al. 2019) as the interpretation of success can often be confounded by a lack of pre-disturbance information (Verdonschot et al. 2013). This can lead to shifting baselines (Pauly 1995), where the degraded conditions known to the current generation anchor what the environment 'should' look like even if conditions were far different a generation earlier. Selection of appropriate reference targets is also key to appropriate assessment of success. White and Kaplan (2017) suggested selecting sites that may not be 'pristine' but that reflect the broad-scale perturbations in the area (e.g., the dynamic reference concept; Hiers et al. 2012). In addition, because recovery trajectories can be complex and nonlinear, and recovery may be to a new alternative state, long-term monitoring and objective criteria are needed for assessment (Clements et al. 2010; Stanley et al. 2010; Duarte et al. 2015; Zhao et al. 2016).

A consistent theme in restoration is that there is seldom full recovery after degradation (Simenstad et al. 2006; Elliott et al. 2007, 2016; Palumbi et al. 2008; Lotze et al. 2011; Shade et al. 2012; Verdonschot et al. 2013; Duarte et al. 2015), suggesting that hysteresis and multiple ecological states may be common. Simenstad et al. (2006) indicated that wetland restoration efforts yielded only partial function. In coastal areas, recovery of faunal groups and habitats was often incomplete and took decades (Lotze et al. 2011; Duarte et al. 2015). Shade et al. (2012) found that very few disturbed microbial communities recovered to their original state. Similarly, lake recovery after phosphorus removal can take decades (Scheffer et al. 1993; Carpenter et al. 1999; Jeppesen et al. 2005). For most systems, lags in recovery after implementation of restoration activities should be expected (Simenstad et al. 2006; Duarte et al. 2015; Lin et al. 2019), suggesting that expectations of management effectiveness should incorporate these lags.

Restoration appears to be most effective when there is an understanding of the stressors impacting the system and how the natural system behaved in the absence of those stressors.

Recovery will depend on the type and intensity of the stress as well as correspondence with natural events and causative stressors may need to be reduced to levels much lower than those that caused degradation due to hysteresis (Duarte et al. 2015). Physical and chemical variables may interact to enhance, or retard impacts of stress. Low salinity was shown to buffer the impacts of increasing nutrients in lagoonal systems, while at higher salinities, the system shifted to a turbid water state (Jeppesen et al. 2007). Removing eutrophication stress may allow ecosystems to be resistant to higher temperatures, salinity variability, disease, storms and invasive species (Wainger et al. 2017). Understanding the underlying physical and chemical factors influencing the ecological system will be critical when determining appropriate management action. Recovery from acute stressors may be quicker than from chronic stressors (Elliott et al. 2007). Distinguishing stressors that can be directly controlled from those over which managers have no direct control, such as climate change will also be critical (Verdonschot et al. 2013), especially since climate change is changing ecological baselines (Duarte et al. 2015).

Many authors highlighted the importance of protecting, enhancing or preserving natural features, processes and functions (Simenstad et al. 2006; Elliott et al. 2007, 2016; Waples et al. 2009; Verdonschot et al. 2013; Duarte et al. 2015; Timpane-Padgham et al. 2017). Accounting for current or matching historical variability of abiotic drivers and ecological processes will increase resilience of the restoration (Waples et al. 2009; Truchy et al. 2015; Zhao et al. 2016). Hydromorphology is a major structuring variable in aquatic systems (Elliott and Whitfield 2011; Elliott et al. 2016; Zhao et al. 2016; Zedler 2017; Amelie and Creed 2018; Arthington et al. 2018). Restoration of parts of the natural flow regime will help restore biodiversity and ecological processes (Arthington et al. 2018). Freshwater flow to estuaries is a major structuring factor; those with less freshwater inflow tend to be more sensitive than those with large flow (Zedler 2017). Similarly, hydrologic resilience of watersheds may be enhanced by restoring freshwater wetlands; any wetland can help with drought, but only riparian wetlands help with floods (Ameli and Creed 2018). In addition to hydrology, restoration efforts should focus on other factors known to increase resilience. Life history diversity rather than overall stock abundance should be prioritized along with habitat heterogeneity (Waldman et al. 2016), and floodplain connectivity (Timpane-Padgham et al. 2017). Success of restoration should consider local and regional context in addition to the particular site to ensure that natural disturbance regimes are restored so that a mosaic of communities is more likely to develop (Sinclair et al. 2018; Janssen et al. 2019). Site-specific factors may be important as well. Elliott et al. (2007) suggested that restoration may be enhanced through the use and protection of keystone species

and ecological engineers. Site characteristics may act as an environmental filter; invasive species may be present in large numbers in seedbanks, while nearby intact wetlands may be a source of native propagules (Hazelton et al. 2018).

Many authors indicated that stakeholder involvement was critical for restoration success (Elliott et al. 2016; Waldman et al. 2016; Christie et al. 2018; Kibler et al. 2018; Krievins et al. 2018). While several authors suggested that including stakeholder involvement can improve restoration effectiveness (Christie et al. 2018; Krievins et al. 2018), they may also limit restoration either through necessary trade-offs (Elliott et al. 2016; Alexander et al. 2016) or because of a desire to maintain the current, unrestored state (e.g., reservoirs behind dams; Kibler et al. 2018). It is also important to remember that stakeholders may value and experience a place differently depending upon class, gender or race (Kibler et al. 2018) and that it takes time and money to develop relationships and trust needed for successful restoration (Christie et al. 2018).

## Management

There is tremendous uncertainty when managing aquatic systems. We seldom know the precise mechanisms that maintain desired conditions, regulatory mechanisms may target different aspects of the systems in conflicting ways, and cultural and economic pressures may not support desired aquatic conditions. Uncertainty and ‘hedging’ should be incorporated into management by managing for heterogeneity (e.g., multiple habitats, functional redundancy and response diversity) or implementing a portfolio of management interventions (Hughes et al. 2005; Schindler and Hilborn 2015; Truchy et al. 2015; Penaluna et al. 2018). Because restoring natural disturbance regimes may not be possible due to social system constraints, it may be necessary to manage for processes that emulate natural disturbance to produce habitat heterogeneity (Penaluna et al. 2018). Considering the socioecological system on a landscape scale while incorporating uncertainty will help ensure that management can be responsive in the face of an uncertain future (Beller et al. 2019). Incorporation of variability into management frameworks will increase resilience. Reeves and Duncan (2009) suggested management goals not be based on a mean of historical variability but rather the variability of the system (high and low thresholds) given current environmental conditions.

Ecosystems are affected by and respond to disturbances on multiple scales. Additionally, the system may be managed at multiple scales, through multiple organizations with different management goals. Although adding complexity, this may allow for more effective management (Gunderson 2000). Even if management actions focus on a local area, assessment of the larger landscape will be required

(Poiani et al. 2000; Hughes et al. 2005; Beller et al. 2019). For example, while local management efforts may improve coral health, the global pressures of climate change and ocean acidification will place an upper limit on coral reef resilience (Anthony 2016). Management of inland freshwater waters should incorporate the watershed. Management of estuary condition or salmon stocks should include measures to enhance resilience in the estuary as well as the watershed and oceanic system (Bottom et al. 2009; White and Kaplan 2017; McCleod et al. 2019). Temporal scales for management need to be expansive enough to track the resilience of key ecosystem services and need to be paired with monitoring that encompasses natural seasonal cycles and is long enough (decades) to see ecological trends. Effective monitoring encompassing spatial and temporal scales allows determination of the effectiveness of management interactions on the system (Arnold et al. 2014; Schindler and Hilborn 2015). A mismatch between the temporal or spatial scale of ecological area and the institutional level responsible for management may adversely impact resilience (Maciejewski et al. 2015).

Management for specific goals or optimal conditions can decrease or minimize other ecological functions, decreasing resilience and increasing system vulnerability to stressors that might otherwise have been absorbed (Peterson et al. 1998). However, managing for ecosystems services may support resilience (Folke et al. 2004; Bottom et al. 2009). For example, improved lake water quality is related to resilience and improved ecosystem services (Carpenter and Cottingham 1997). Similarly, increased biodiversity is positively related to ecosystem services (Birge et al. 2016). However, optimizing the social system to maximize ecosystem services may lead to overexploitation of the ecological system unless the ecology is well understood (Hughes et al. 2005). Reducing the fishing fleet did not increase salmon stocks but did adversely impact the livelihood of coastal fishers; managing to maximize community and cultural resilience may lead to better outcomes (Healey 2009). Because there is no optimum level of ecosystem services, trade-offs need to be made at multiple scales which balance the desires of diverse, competing groups (Robards et al. 2011; Birge et al. 2016; Berkes 2017) although ecological models may assist in examining some of these trade-offs (Weijerman et al. 2018).

Adaptive management may help with these issues detailed above (Gunderson 2000; Schindler and Hilborn 2015) as it is multidisciplinary, so more than one perspective is incorporated, and iterative, so that decisions can be made even in the face of uncertainty and unpredictability. Carpenter and Gunderson (2001) showed that adaptive management increased resilience and stabilized system behavior. Two facets of adaptive management are inclusion of stakeholders, and management by multiple entities at multiple scales (Hughes et al. 2005; Camp et al. 2015; Thom et al. 2016; Peat et al.



2017; Zedler 2017). Although this inclusion is desirable, the time and money costs of involving multiple stakeholders and governance bodies must be considered (Biggs et al. 2015; Thom et al. 2016; Peat et al. 2017). Because management agencies are constrained by their laws and policies, adaptive management can be implemented in limited areas, with the support and flexibility of agency managers (Thom et al. 2016; Peat et al. 2017). Employing stakeholders to implement multiple potential restoration experiments is one way to encourage buy-in and increase resilience of the system (Camp et al. 2015). Adaptive management also requires monitoring encompassing spatial and temporal scales to allow determination of the effectiveness of management actions (Arnold et al. 2014; Schindler and Hilborn 2015; Thom et al. 2016; Peat et al. 2017; Zedler 2017).

## Conclusions

Meeting societal expectations for aquatic systems and the ecosystem services they provide is a growing challenge. Understanding socioecological resilience and managing systems to enhance resilience will be critical to meet this challenge but will not be easy. As outlined in this review, many factors interact across scales and in complex ways to influence the ability of aquatic systems to absorb and respond to stressors and disturbance. Furthermore, managing for aquatic socioecological resilience will be fraught with social conflict given the inevitability of tradeoffs among valued ecosystem services and the reality that different segments of society are dependent to varying degrees on these services.

Our review revealed evidence for the importance of managing stressors adversely impacting aquatic system resilience, as well as understanding the environmental and climatic cycles and changes impacting aquatic resources. Resilience may be strengthened by maintaining and enhancing habitat connectivity as well as functional redundancy and physical and biological diversity. These factors interact with each other to maintain metapopulations and provide 'insurance' against environmental changes. Resilience in aquatic socioecological system may be enhanced by understanding and fostering linkages between the social and ecological subsystems and understanding how the system is impacted by factors within and outside the area of immediate interest. Within the social system, collaborative and adaptive management can result in a system that works to optimize and equitably distribute ecosystem services, especially if stakeholders have a good understanding of the underlying ecological systems. Restoration may help to recover ecosystem services but is likely to be incomplete and characterized by lags in response. Management of the ecological system requires understanding of how the system functions,

including incorporation of uncertainty and scalar issues, as well as understanding the social pressures upon the system.

In order to effectively implement adaptive management of aquatic systems for resilience, monitoring to detect changes in the socioecological system will be needed. In addition, research will continue to be needed to: (1) inform development of sensitive indicators and monitoring designs (2) disentangle complex multi-scalar interactions and feedbacks that currently limit our ability to foresee outcomes of management decisions and stressors, and (3) help generalize lessons learned across aquatic ecosystems as adaptive management progresses and apply them in new contexts.

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