Reservoir Fish Habitats: A Toolkit for Coping with Climate Change

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Abstract.-- Climate change is the defining environmental problem for our generation. The effects of climate change are increasingly evident and anticipated to profoundly affect our ability to conserve fish habitats and fish assemblages as we know them. Preparing to cope with the effects of climate change is developing as the central concern of aquatic resources conservation and management. Reservoirs are important structures for coping with projected shifts in water supply, but they also provide refuge for riverine fishes and retain distinct fish assemblages that support diverse fisheries. The effects of climate change on reservoirs are unique among aquatic systems because reservoirs have distinctive habitat characteristics due to their terrestrial origin and strong linkage to catchments. We review (1) the projected effects of rising temperature and shifting precipitation on reservoir fish habitats, and (2) adaptation strategies to cope with the anticipated effects. Climate warming impacts to reservoirs include higher water temperatures and shifts in hydrology that can result in reduced water levels in summer and fall, altered water residence cycles, disconnection from upstream riverine habitats and backwaters, increased stratification, eutrophication, anoxia, and a general shift in biotic assemblages including plants, invertebrates, and fishes. We suggest that what is needed to cope with these changes is a new perspective focusing on maintaining ecosystem functionality rather than on retaining a particular species composition. To that end, we offer a toolkit organized into planning, monitoring, and managing compartments, and equipped with 22 adaptation tools. The coping strategies we identify are broad and general and represent a starting line applicable for developing creative alternatives relevant to local conditions.

1. Introduction

Apparent signs of climate change are perhaps the most defining environmental issue of this generation. The effects of climate change are increasingly evident, from melting glaciers and coastal flooding to drying lakes, torrential downpours, and expansions and contractions of species' distributions (Melillo et al. 2014). These and other changes are bellwethers for what climate scientists anticipate will be dramatic impacts in decades to come (Maclean and Wilson 2011). The projected climate will profoundly affect our ability to conserve fish habitats and fish assemblages as we know them. Preparing for and coping with the effects of climate change is emerging as the overarching concern of aquatic resources conservation and management. Nevertheless, climate change is a slowly evolving and uncertain phenomenon. Unlike a major disaster, such as an earthquake or a hurricane, the slow progression of climate change has not catalyzed decisive action in part due to societal difficulties dealing with programs that require huge investments upfront to avoid unknown risks in decades to come.

Reservoirs are important artificial structures for coping with anticipated temporal shifts in water supply (Christensen et al. 2004). Next to water storage, reservoirs provide seasonal refuge for some riverine species and support distinct fish assemblages that provide diverse recreational, commercial, and subsistence fisheries. The effects of climate change on reservoirs are unique among aquatic systems because reservoirs have specific habitat characteristics due to their terrestrial origin and strong linkage to catchments (Knoll et al. 2003). Unlike natural lakes, reservoirs tend to have large catchments and large tributaries because they were engineered to capture as much water as possible. This origin is manifested by relatively large inputs of inorganic and organic loads. Depositional filling effectively results in relatively rapid surface area and volume reductions, habitat fragmentation, loss of depth, and associated changes in water quality (Patton and Lyday 2008; Miranda and Krogman 2015). Unnatural water-level fluctuations degrade shorelines that were once uplands and therefore maladapted to regular flooding, promoting erosion and ultimately homogenization of once diverse nearshore habitats (Miranda 2017). Wellestablished riparian zones and floodplain wetlands that provide key ecological services to natural lakes and the original river are mostly missing in upland reservoirs. Lack of woody debris deposition, limited access to backwaters, and lack of seed banks and stable water levels that discourage native aquatic vegetation often produce barren littoral habitats. Because of their artificial origin, reservoirs reveal unique fish habitat problems that stand to be compounded by anticipated shifts in climate.

We review (1) the projected effects of climate change on reservoir fish habitats and (2) adaptation strategies that could help reduce, ameliorate, or otherwise cope with the anticipated effects of climate change on reservoir fish habitats. We have not assembled an exhaustive inventory. Instead, the effects we describe represent the most likely ones. The strategies we list are broad and general and represent a starting line applicable at the agency or regional level for developing creative alternatives relevant to local reservoirs and climate conditions.

2. The Shifting Climate

Global mean surface temperatures have been rising over the last two centuries, with mean land and ocean temperatures warming an average 0.9°C during 1880-2012 (Hartmann et al. 2013). Freshwater lotic systems have been exceptionally vulnerable to warming, with major rivers and streams in the U.S. warming at a rate of 0.1-0.8°C per decade (Kaushal et al. 2010). Lentic systems have also been warming and is most evident in colder latitudes where ice-breakup has on average occurred 7-d earlier and freezing 6-d later per century (Vincent 2009). Temperatures are predicted to continue to rise in the 21st century, although by 2020 the climate change signal may not be clearly distinguishable from the effect of natural long-term climatic variability.

Representative Concentration Pathway (RCP) assessment models of climate change adopted by the IPCC (2019) anticipate global temperatures to increase by an average 1.1-2.6°C by late-century under the RCP4.5 model, and by 2.6-4.8°C under the RCP8.5 model. RCP models account for climate dynamics and real-world factors like population growth, environmental policy, and development of new technologies. There are four total RCP models used by the IPCC, and we selected two because they sufficiently cover the range of most probable scenarios. RCP4.5 represents a moderate effect and assumes a worldwide effort to reduce emissions by roughly 50% by the end of the 21st century via policy changes and technological developments, leading to CO₂ emissions peaking mid-century and declining thereafter. RCP8.5 represents a high effect if there are no policy changes to reduce emissions, and only modest technological improvements and behavioral changes. These potential increases in temperature also affect precipitation and therefore the amount and timing of water that reaches reservoirs and water quality.

Substantial changes to the water cycle are expected as the planet warms because movement of water in the atmosphere and oceans is a primary mechanism for how heat is distributed around the planet. A warmer climate increases evaporation of water from land and sea and allows more moisture to be held in the atmosphere. Climate change is predicted to continue to alter the timing and quantity of global precipitation. Total precipitation in the mid-latitudes of the northern hemisphere has been increasing since at least 1901 (Hartmann et al. 2013). In the U.S., drought length and frequency have decreased, except in the Southwest and interior West where they have increased (Andreadis and Lettenmaier 2006). Climate change is predicted to increase global precipitation, but precipitation will be concentrated over shorter periods (Collins et al. 2013). Generally, the result of these shifts will be an intensified hydrologic cycle of high-flow events and flooding interspersed with drought (Kirtman et al. 2013).

Climate predictions often have large uncertainty. Climate fluctuates due to internal variability (e.g., El Niño/Southern Oscillation) and external forces (e.g., volcanic eruptions) (Kirtman et al. 2013). Climate predictions are based upon reference and historical climatic conditions that incorporate these sources of internal and external variability to forecast future trends (e.g., RCP models). There are many factors that influence the outcomes of simulations, some of which may change over time and are difficult to predict, such as socioeconomic development of large countries that influence the extent of greenhouse gas emissions (Arnell and

Hulme 2000). Small differences in the initial parameters of models can make big differences in predictions, sometimes leading to substantially different outcomes. In general, the projected changes in precipitation are less certain than those for temperature.

2.1 Regional patterns across the U.S.

Shifts in temperature and precipitation are projected to show regional differences in the U.S. (Figure 1). Increases in temperature are likely to be strongest inland and at higher latitudes, with lesser warming near the coasts. Warming is likely to be especially pronounced at higher latitudes in winter. Changes in atmospheric circulation will tend to move storm tracks northward

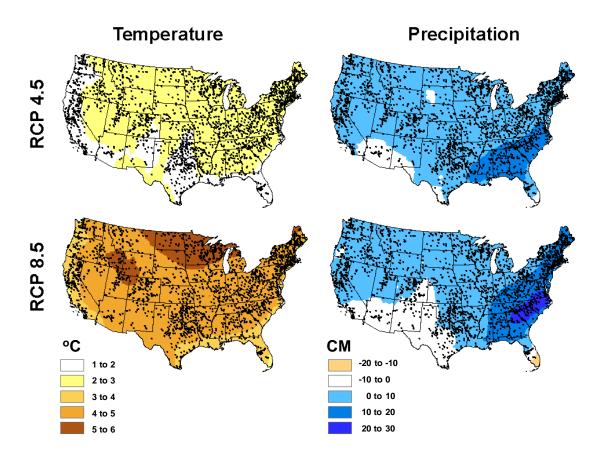


Figure 1. Projected change in annual mean temperature (°C) and precipitation (cm) across the conterminous U.S. Projections are for the year 2091 and changes are relative to the reference period 1986-2005. The Representative Concentration Pathway (RCP) assessment model RCP4.5 represents a moderate effect that assumes a worldwide effort to reduce emissions by roughly 50% by the end of the 21st century, leading to CO₂ emissions peaking midcentury and declining thereafter. RCP8.5 represents a high effect likely if there were no policy changes to reduce emissions, and only modest technological improvements and behavioral changes. Dots identify distribution of reservoirs larger than 100 ha.

causing dry regions to become drier and wet regions to become wetter (Jain et al. 2005; Pagano and Garen 2005; Hamlet and Lettenmaier 2007). Thus, even though temperature and total precipitation increases, the regional and seasonal distribution of these variables are expected to change. Also, more precipitation is projected to come in heavy downpours rather than soaking events (Furniss et al. 2010).

Increases in annual precipitation, runoff, and soil moisture are expected in the Southeast, Northeast, much of the Midwest, Northern Plains, and Northwest, and declines in the Southwest, and parts of the Southern Plains and West (Figure 1). The arid Southwest is projected to experience longer and more severe droughts from the combination of increased evaporation and reduced precipitation. The frequency of droughts is projected to increase in Southeast and Rocky Mountain states (Strzepek et al. 2010). Changes from snow to rain are expected primarily at the lowest extent of current snow lines (Knowles et al. 2006). Most scenarios project a combination of less earlywinter snowfall and earlier snowmelt leading to a longer growing season, earlier peak river flows, and more water being transported during the spring and less during the summer and fall (USBR 2008; Karl et al. 2009; Ehsani et al. 2017). The impacts will likely include too little water in some regions of the U.S., and too much in others. Some regions are expected to be subject to all these conditions during different times of the year. Despite increased precipitation in some regions, annual water availability in reservoirs may decline under most climate scenarios due to the increase in evapotranspiration (Ehsani et al. 2017).

2.2 Climate change and reservoirs

Climate warming impacts to reservoirs include higher water temperatures, more evapotranspiration, and shifts in hydrology (Ehsani et al. 2017) that can result in lower dissolved oxygen and less water, thus shifting biological assemblages and causing fish kills (Figure 2). Impacts also include reduced reservoir levels in summer and fall, loss of habitat, disconnectedness from upstream riverine habitats and adjacent backwaters, and loss of recreational access. In the southern U.S., reductions in the frequency and intensity of cold winter temperatures can allow tropical and subtropical fishes to move northward and replace some temperate species. Where climatic thresholds are crossed, certain ecosystem and landscapes may be transformed by warming winter temperatures. Increased precipitation and soil moisture in a warmer climate also lead to increased loss of soil carbon and degraded surface water quality due to loss of soil particles and nutrients (Davidson and Janssens 2006). Transitions from extremes of drought to floods increase nitrogen inputs into reservoirs and can lead to harmful algal blooms (Chapra et al. 2017).

3. Effects on Integrity of Reservoir Environments

Changes in climate are projected to transform reservoir fish habitats through various direct and indirect pathways. For convenience, we categorize the projected transformations as changes

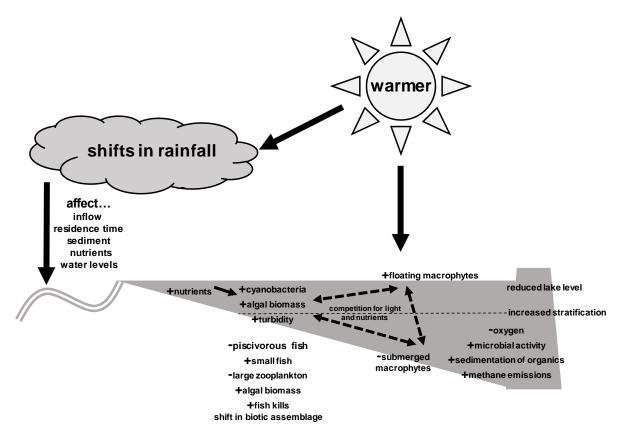


Figure 2. Climate warming impacts to reservoirs include higher water temperatures and shifts in precipitation and hydrology that can result in altered physicochemical characteristics leading to changes in biological assemblages.

to the physical, chemical, and biological environments (Table 1), although these categories are intertwined. Together, these major classes influence fish assemblages in loosely predictable ways.

3.1 Physical integrity

3.1.1 Catchment

Climate change can impact reservoir catchments through influences on soil properties and vegetation composition, leading to changes in reservoir sediment loadings and water storage capacity. Soil moisture in catchments is predicted to be altered by changes in temperature, evapotranspiration rates, and runoff. Erosion of catchment and reservoir tributaries can be intensified by more frequent and severe high-flow events, polarized wet/dry seasons, and distressed vegetation communities (Furniss et al. 2010; DEFRA 2013). Changes in seasonal temperature and precipitation may increase forest mortality and wildfires that alter vegetative communities in the catchment and the reservoir's riparian contour (Furniss et al. 2010).

Temperature rise and shifts in precipitation can lead to geographic changes in composition of various forest types (Saetersdal et al. 1998). Long-term contributions to the reservoir basin by organic particulate matter and coarse woody debris from forested landscapes may be affected by these changes. Vulnerability of catchments to increasing temperatures and changing precipitation pose a risk to reservoirs.

Changes in precipitation brought by climate warming could alter the distribution of agriculture and forestry as land use within a basin may be converted to or from cropland depending on the occurrence of drought (Boehlert et al. 2015). For example, in some cases climate change may facilitate expanding agricultural areas in higher latitudes or changing the types of trees grown in managed forests, altering patterns of runoff from the catchment into reservoirs. These changes in land use would have direct and indirect influences on reservoir ecosystems. For example, if agricultural land uses increase in importance, the likely consequence is increased loads of sediment and nutrients, and associated water quality changes related to such inputs (Miranda 2017). The conversion of forest vegetation in riparian zones to agricultural land would also exacerbate the effects of warming on reservoirs because riparian shade creates unique water quality microhabitats that help promote fish assemblage diversity in nearshore contours of reservoirs (Raines and Miranda 2016; Miranda and Raines 2019).

Suspended sediment, sedimentation, and eutrophication are major problems in many reservoirs and are often linked to sediment and nutrient availability in the catchment and to transport capacity provided by runoff. Increased seasonal high flows anticipated in some regions of the U.S. are likely to lead to increased transport of sediment and nutrients into reservoirs. There is considerable uncertainty regarding the effects of climate change on sediment erosion and nutrient delivery, but it can be projected that in many catchments an increase in rainfall and runoff will be associated with an increase in reservoir seasonal turbidity and sedimentation (Arnell and Hulme 2000). Even where average rainfall decreases, an increasing frequency of intense rainfall separated by drought could increase suspended sediment and sedimentation in reservoirs (DEFRA 2013). These sediment increases may reduce reservoir lifespan (Palmer et al. 2008) and impair trophic status and have major repercussions on fish habitat degradation, with lopsided effects on shallow littoral areas of reservoirs (Patton and Lyday 2008; Miranda and Krogman 2015).

Runoff is the amount of precipitation that is not evaporated, stored as snowpack or soil moisture, or filtered down to groundwater. The percentage of precipitation that runs off through the catchment is determined by a variety of factors including temperature, vegetation, and soil moisture (Jeppesen et al. 2009). While runoff generally reflects precipitation, increases and decreases in precipitation do not necessarily lead to proportionate changes in runoff (Linsley 1967). For example, droughts cause soil moisture reductions that can reduce expected runoff until soil moisture is replenished. Conversely, water-saturated soils can generate floods after only moderate precipitation. Climate models consistently project that catchments in the eastern U.S. will experience increased runoff, while there will be substantial declines in the interior West, and especially in the Southwest.

3.1.2 Horizontal habitat connectivity

Reductions in water levels due to drought, and excessive sedimentation due to torrential rains, can alter connectivity to lateral aquatic habitats, particularly in shallow lowland reservoirs (Patton and Lyday 2008; Miranda 2017). Water bodies including tributaries adjacent to reservoirs are used by many reservoir species for spawning and nursery sites, by permanent reservoir residents, and by species that live in the reservoir or tributaries seasonally or during specific life stages. Drought can isolate backwaters from the main reservoir and from each other. With the projected increases in the intensity and frequency of drought across much of the U.S., lateral disconnection from neighboring water bodies and riparian habitats will likely become more common for many reservoirs across the country. Torrential rains move sediment that generally settles near the mouth of tributaries as water enters the reservoir. Loss of connectivity also develops in shallow embayments and major tributaries through fragmentation created by the combination of sediment deposition and accretion (Patton and Lyday 2008). As embayments of the reservoir become filled with sediment, water that flows into the reservoir helps to form channels by depositing sediment on both sides of the flow channel. As discharges exceed the banks, water spills out of the channel, losing much of its energy and allowing sediment to fall out of the water column and deposit adjacent to the channel. Over time, this process tends to separate the channel from the backwaters and isolate backwaters. This isolation can change the makeup of reservoir fish assemblages (Patton and Lyday 2008). Under a changing climate that is projected to have more concentrated and intensified wet seasons, habitat fragmentation and isolation may be worsened or accelerated in reservoirs via alterations to sediment transport, deposition, and accretion pathways.

3.1.3 Storage

Increasing temperatures are expected to reduce the amount and extent of snow cover, with the biggest influence at the margins of regions where snow currently plays an important role. The duration of snow cover is projected to be diminished across the northern U.S., affecting timing of streamflow and storage, as precipitation that falls as rain during winter or spring runs off, rather than being stored as snow to melt the following spring (Arnell and Hulme 2000). Instead, runoff is projected to occur earlier in the year reducing late-summer runoff. In some regions existing reservoirs may be incapable of storing the added early water resulting from rain and snowmelt to later counter lower inflows in dry months, leading to overall lower water levels in late-summer and fall (Ehsani et al. 2017). Thus, earlier runoff produces lower late-summer inflows, which stress reservoir habitats through less water availability later in the year and overall higher water temperatures.

The projected changes in temperature and precipitation are expected to affect the current water supply-demand balance and challenge current reservoir water management strategies (Ehsani et al. 2017; Rahmani et al. 2018). The hydrological implications of precipitation changes are that the original storage and release designs may need adjustments to accommodate higher or lower inputs, and to accommodate timing including seasonality, torrential short-term events, and earlier snowmelt. The vulnerability of reservoirs to floods and droughts will likely increase, and the trade-offs between reservoir releases to maintain flood control storage, drought resilience,

energy production, and suitable depth for navigation and fish requirements will need to be reconsidered. The need to release otherwise valuable water may require reassessing the trade-offs between having a flood and drought resilient system and meeting in-lake and downstream water demands as these goals compete to utilize the same limited reservoir storage. Ehsani et al. (2017) suggested that in addition to modifying reservoir operations, it may be necessary to increase the size and number of reservoirs. Many reservoir storage challenges will be exacerbated by the shrinkage of storage space caused by the accelerated sedimentation expected in various regions of the U.S. (Wisser et al. 2013).

3.1.4 Water residence time

Increased drought frequency and duration coupled with heavier precipitation pushed back from spring to winter may require longer residence time to store water from wet to dry seasons. Predictions are that flood risk will increase due to more intense precipitation events and more precipitation falling as rain instead of snow. In agricultural regions precipitation may arrive in reservoirs too early for use in agricultural diversions and must be stored longer (USBR 2008). Residence time affects the chemical composition of the water by controlling the time available for biogeochemical and photochemical processes to operate, the extent of accumulation and loss of dissolved and particulate materials, and the duration of biogeochemical interactions with sediment (Vincent 2009). In reservoirs that stratify, a prolonged residence time can result in accelerated eutrophication (more in section 3.2). Conversely, phytoplankton production may be compromised in regions that experience reduced residence time due to increased precipitation, which is often associated with increased turbidity and flushing of nutrients (Ambrosetti et al. 2003; George and Hurley 2003). Reduced residence and associated flushing of nutrients may be offset by fast-tracked transport of nutrients into the reservoir.

3.1.5 Water level fluctuations

Water level is directly related to storage and is a key habitat variable for fishes that use nearshore contours for at least a portion of their lifecycle. Reservoir water levels are often regulated by "rule curves" or "guide curves" that require a certain amount of storage space to be saved in a reservoir at certain times of the year to capture potential floods. Guide curves are engineered based on historical records of stream inflows, lake levels, precipitation, and water demand (Yeh 1985; Mower and Miranda 2013a). Most aspects of water management including reservoir sizing, reservoir flood operations, and projected water demands have been based on these records. Because climate change will significantly modify many aspects of the water cycle, past assumptions derived from the historical record about supply and demand will need to be revisited. The flexibility to modify guide curves will be critical for the protection of infrastructure, for public safety, to ensure reliability of water delivery, and to protect fish assemblages and fisheries. There are, however, many institutional and legal barriers to such changes. Guide curves have not been easily changed as oftentimes modifications require congressional approval (Mower and Miranda 2013b). Not only do most guide curves not account for climate change impacts, but they also fail to take advantage of modern technical tools that allow for more flexible reservoir management

(Willis et al. 2011). These include software that can automatically adjust the extent of releases by integrating current storage levels, weather-forecasting capabilities, data on water content in the catchment, and magnitude of incoming river flow (Ehsani et al. 2017; Zhang et al. 2017).

Increased drought frequencies, intensities, and duration particularly in summer are expected to intensify annual water level fluctuations, mostly in the Southwest and mid-continental regions. Large reservoirs with extensive shallow littoral zones, as well as most small reservoirs, may be impacted by long-term drought conditions in summer and fall that lower water levels and dewater key littoral habitats. When water levels drop, reservoirs with shallow and gently-sloping littoral slopes as well as small shallow reservoirs experience a greater magnitude of change than those with steep slopes (Stamou et al. 2007). These periodic drawdowns typically create barren shorelines with low habitat diversity and depressed species richness (Jeppesen et al. 2015; Hatcher et al. 2019). Excessive water level fluctuations also create environments dominated by turbid water (Zohary and Ostrovsky 2011). Excessive fluctuations and barren littoral zones may limit development of littoral species in favor of pelagial fish species.

Reductions in water level are also likely to accelerate eutrophication processes through various pathways (Persson et al. 1991; Jeppesen et al. 2000). Like waves in the ocean that break at the sea shore, wind-induced waves in reservoirs break when they hit the sloping shore of the lakebed, causing turbulent mixing, sediment resuspension, and release of nutrients deposited in the uppermost sediment layers. Another eutrophication impact of extreme water level reduction may be the proliferation of mid-summer full water column mixing events, such as when episodes of intense rainfall lead to turnover and nutrient releases into the epilimnion.

Increased exposure of littoral habitats in summer and fall due to shifts in seasonal precipitation, increased evaporation, and the need for increased withdrawals to mitigate drought could allow encroachment of upland vegetation into exposed areas. Often the type of upland vegetation that thrives in exposed areas tend to be invasives. This vegetation can potentially enhance selected reservoir fish populations as various studies have shown that flooding riparian vegetation provides food and cover for juvenile fish (Miranda et al. 1984; Mitzner 1991). Nevertheless, if the vegetation is dewatered in early summer because of drought, it may provide habitat for spawners but not cover and access to macroinvertebrate prey to support juvenile fish production.

3.2 Chemical integrity

3.2.1 Stratification

In reservoirs with limited flows, higher surface temperatures lead to earlier onset and longer periods of stratification (i.e., when surface and bottom waters do not mix). Deep stratified reservoirs usually mix or turnover in spring and fall (dimictic) or fall only (monomictic). During periods of strong stratification, the lower layers of the water column become isolated from the atmosphere and a vertical density gradient acts as a barrier to mixing (Wetzel 2001). Without

mixing to replace dissolved oxygen, the deeper water layers, lacking enough light for photosynthesis, tend to have no or limited oxygen. Biotic respiration further assists in depletion of the dissolved oxygen in the lower layers (Peeters et al. 2002). The circulation created by seasonal turnover moves oxygen from the surface to the deeper layers and resuspends nutrients previously trapped in the hypolimnion. The onset of stratification is postponed by inflows but exacerbated by reduced inflows and warmer temperatures. The mixing regime strongly affects nutrient loadings, phytoplankton abundance, and lake water chemistry. The effects of climate warming on the thermal structure of reservoirs and nutrient circulation are expected to be equivalent to considerable increases in the external nutrient loading and upgrade eutrophication status of many reservoirs (Trolle et al. 2011).

Increased epilimnetic temperatures are expected to strengthen stratification, intensify hypolimnetic oxygen depletion, and possibly increase hypolimnetic temperatures (Jankowski et al. 2006; Modiri-Gharehveran et al. 2014). Seasonal hypolimnetic changes in dissolved oxygen could be more conspicuous in oligotrophic reservoirs because eutrophic reservoirs will already have low epilimnetic dissolved oxygen. With longer stratification, bottom hypoxia will likely develop earlier in the year, last longer, and cover a greater spatial extent. Water quality simulations have shown that because of warming, dissolved oxygen concentrations in the epilimnion may decrease by <2 mg/L, but hypolimnion concentrations may decrease by much more (Stefan et al. 1993; Stefan et al. 2001), resulting in increased frequency of anoxia in bottom waters during mid- and late summer. Some climate scenarios predict warming epilimnion temperatures that could cause a cooling hypolimnion (De Stasio et al. 1996). By trapping heat at the surface layer, less heat is available for warming the lower column, and deep waters can become cooler because of climate warming, at least in some reservoirs.

The suitability of the hypolimnion as a thermal refuge for some reservoir fishes can be reduced by prolonged and strengthened stratification. Coolwater stenotherms, such as striped bass *Morone saxatilis* and various salmonids, use the hypolimnion as a refuge from high summer water temperatures (Christie and Regier 1988; Coutant 1990). Fishes that seasonally depend on the hypolimnion for suitable temperatures can be faced with a "temperature-oxygen squeeze" where they are vertically confined to a habitat bounded by the warm temperatures in the epilimnion and the low dissolved oxygen levels in the hypolimnion (Coutant 1985). This severely limits their habitat during warm months. When thermal refugia are reduced in volume, the fish are crowded into a smaller amount of water with higher likelihood of rapid oxygen depletion, low prey availability, stress, and disease transmission (Chang et al. 1992).

3.2.2 Water quality

Climate change is likely to have far-reaching effects on overall water quality in U.S. reservoirs due to increases in water temperature, reduced vertical mixing, added biotic respiration, and decreases in dissolved oxygen that influence a multiplicity of chemical reactions. Water quality in reservoirs is projected to decrease across the majority of the country (USEPA 2017), particularly in the Northeast, Southeast, and Midwest regions, primarily due to the interaction of increased temperature, seasonally high/low precipitation fluctuations, and nutrient loadings. Reduced water quality is projected to affect the ecological dynamics of reservoirs, with cascading effects on fish assemblages and recreational opportunities, including fishing.

The effects of water pollution, including sediment, nitrogen, phosphorus, and pesticide loadings could be amplified by projected seasonal changes in precipitation in most of the U.S. Heavy downpours earlier in the year when sun angle is low (climate change will not affect sun angle and photoperiod) and thus vegetative cover (leaves and ground cover) is light can lead to increased delivery of sediment and nutrients (Arnell and Hulme 2000). Loadings will likely increase in the spring, when precipitation and the loading potential are higher, owing to agricultural fields being fallow or the crops not yet mature. Conversely, phosphorus loading will likely decrease in the summer when precipitation is lower and the crops will be actively taking up phosphorus. Increased delivery of pollutants into reservoirs, coupled with reduced flow, water level, and increased temperature later in the year can result in blooms of bacteria and harmful algae. However, predictions are uncertain because pollution can potentially be diluted in those reservoirs that experience heavy seasonal inflows. Nevertheless, the U.S. Environmental Protection Agency is expecting the number of reservoirs considered impaired by water pollution will increase (USEPA 2017).

3.2.3 Eutrophication

The trophic state of reservoirs is a function of depth, water residence time, nutrient enrichment from the catchment, and other related factors (Kalff 2000). Compared to lakes, reservoirs tend to have a fast rate of eutrophication given their often high catchment-to-reservoirarea ratios. Eutrophication is further enhanced by the input of excess nutrients from agricultural and urban runoff and from sewage discharge (Klapper 1991). Although the complex relationship between climate warming and eutrophication makes predictions difficult, increased temperatures could result in a general increase in reservoir trophic status (Allan et al. 2005). Lower stream flows in some regions could increase water residence times and reduce flushing of nutrients. In regions where precipitation is expected to increase, boosted runoff could hasten nutrient accumulation originating from the catchment, but this effect may be countered by the higher flushing rates through the reservoir (Magnuson 2002). Conversely, in some deep reservoirs, climate change could reduce eutrophication as increased strength and duration of stratification could lead to sequestration of nutrients in the hypolimnion, where they are not available to primary producers (Magnuson 2002). There is a lot of contradictory evidence and uncertainty.

One key factor that determines whether the expected increases in temperature and precipitation-driven nutrient loading affect fish production is a reservoir's current trophic status (Moss et al. 2011). In oligotrophic reservoirs where water transparency is generally high, moderate climate-driven increases in nutrient runoff may have mostly positive effects on fish production by promoting plankton (Maceina et al. 1996). Conversely, in eutrophic reservoirs, climate-driven increases in nutrient loading could obstruct fish production by reducing the availability of suitable thermal habitat and prey to fishes during periods of extended bottom hypoxia, or by promoting largely inedible cyanobacteria at the base of the food web (Havens 2008). In eutrophic reservoirs plagued by cyanobacteria blooms, eutrophication could depress fish foraging success, at least during summer and fall (Manning et al. 2014). Thus, while eutrophication is likely to change fish

assemblages, it could have positive or negative effects on fish production in reservoirs, depending on current trophic status.

Water clarity is highly influenced by nutrient and sediment runoff and thus likely to be affected by changing precipitation patterns. In regions where precipitation is expected to enhance nutrient and sediment runoff, changes in turbidity have the potential to alter warming and stratification, depending on factors such as reservoir depth and retention time. Whether reduced water clarity will benefit or harm fish production is difficult to predict, as it depends on many factors, including the nature of the turbidity (sediment or plankton; Wellington et al. 2010), the level of predation risk in the system (Pangle et al. 2007), and on fish assemblage composition.

3.2.4 Anoxia

Next to temperature, dissolved oxygen is arguably one of the principal water quality variables influencing fish assemblages. Increases in temperature will lead to reductions in dissolved oxygen (DEFRA 2013), through reduced solubility in warmer water as well as higher respiration rates of biota (Karl et al. 2009). Further reductions in dissolved oxygen are likely to be caused by nutrient increases and associated algal blooms that (1) tend to increase dissolved oxygen highs, and when they collapse, increase the lows, and (2) intensify diel cycles. Rising temperatures not only reduce dissolved oxygen in the hypolimnion but also in the epilimnion. Dissolved oxygen in the epilimnion is strongly dependent on trophic status -- oligotrophic reservoirs are less affected. Various models predict decreases in dissolved oxygen in reservoirs in the Northeast, Southeast, coastal regions of the Pacific Northwest, and most of the Midwest (USEPA 2017). With mounting anoxia incidents, reservoirs may expect more summer and fall fish kills (Fang and Stefan 1997, 1999). If changing weather patterns produce stronger winds, then there is the risk that the increased mixing of epilimnion and hypolimnion will resuspend anoxic layers and exacerbate anoxia episodes.

3.3 Biological integrity

The responses of biotic aspects to projected physical and chemical changes entangle complex interactions and feedbacks impossible to predict precisely. Nevertheless, some basic direct and indirect effects can be identified as potential impacts of the projected climate changes. These effects occur at various scales, from physiological responses at the individual level to changes in whole reservoir ecosystem structure and dynamics.

3.3.1 Aquatic macrophytes

Many aquatic macrophyte species in the U.S. are limited in range by low winter temperatures, and therefore warming temperatures may facilitate their expansion locally and northward. Higher temperatures can alleviate the latitudinal and altitudinal limitations placed on plants by cold temperatures (e.g., frost kill, dormancy) as well as extend the number of days that plants experience temperatures warm enough to permit growth (Walther 2003). Accordingly,

Jansson et al. (2000) associated longer growing seasons with higher plant diversity and plant density. Warmer temperatures earlier in the year can foster earlier colonization by aquatic macrophytes (Haag and Gorham 1977) and allow some plants to more successfully compete in new habitats, and in higher altitudes and latitudes (Walther 2003). This increased advantage is an important factor when considering the future expansion of exotic plant species such as giant salvinia *Salvinia molesta*, hydrilla *Hydrilla verticillata*, and Eurasian watermilfoil *Myriophyllum spicatum* (Madsen and Owens 2000).

The eutrophic conditions fostered by warmer temperature may stimulate explosive macrophyte growth in some reservoirs. One study reported that a 2-3°C temperature increase could cause a 300–500% increase in biomass of *Elodea canadensis* (Kankaala et al. 2002). Such a large increase in macrophytes would affect a reservoir in various ways. First, because plants take up the nutrients sequestered in the sediment, after the plants die and decompose there would be a large release of nitrogen and phosphorus into the water column (Cooper 1996; Kankaala et al. 2002). Second, this influx of nutrients can stimulate algal and macrophyte blooms and help perpetuate high plant production. Third, the elevated oxygen demand during the bacterial and fungal decomposition of these plants depresses levels of dissolved oxygen in the system, raising the likelihood of fish kills (Klapper 1991), and of stressful oxygen fluctuations that ultimately can shift the composition of fish assemblages.

In contrast to factors that may boost plant growth, water level fluctuations are a primary limiting factor in the abundance of aquatic macrophytes in reservoirs (Poff et al. 1997; Lacoul and Freedman 2006). Increasingly variable water levels like those forecast to occur in some regions could counteract aquatic plant growth, or favor generalist and fast-growing plants over species which thrive in late-succession, stable-stages of aquatic systems (Hudon 1997; Lacoul and Freedman 2006). Invasive species could become favored in reservoirs with fluctuating water levels because of their fast growth rates and lack of natural competitors or predators. The intensity of fluctuations can be as important as their periodicity. Large water level drawdowns tend to reduce submersed and floating-leaved macrophyte abundance. Because aquatic macrophytes generally inhabit the shallow littoral zone, they quickly die when exposed, but propagules may remain (Cooke 1980). Long periods of drawdown associated with drought could cause declines in aquatic macrophyte abundance but would favor growth of moist-soil plants in the exposed littoral areas.

Fluctuating water levels also create unfavorable light conditions via increased turbidity. Light availability is one of the most critical factors determining the establishment of aquatic macrophytes (Chambers and Kalff 1985; Lacoul and Freedman 2006). The projected exaggeration of water levels in reservoirs, combined with the erosive capacity of water level fluctuations, have the potential to seasonally increase turbidity and sediment deposition. Increased waterbody productivity resulting from higher temperatures could also increase turbidity by stimulating phytoplankton growth. Thus, decreased water transparency from either sediment or phytoplankton sources could shrink the size of the littoral zone to reduce aquatic plant growth.

3.3.2 Plankton and cyanobacteria

Changes in light, temperature, and access to nutrients can affect plankton and cyanobacteria species composition and diversity, and in turn impact higher trophic levels (Vincent

2009). A major climate change concern in temperate latitudes is the prospect of a shift in phytoplankton toward dominance by cyanobacteria that form noxious blooms (Moe et al. 2013). Cyanobacteria can create various water quality problems, including the release of disagreeable taste and odor compounds, the production of various toxins, and the overproduction of biomass composed of larger cells that disrupt zooplankton feeding and causes oxygen depletions. Bloomforming cyanobacteria are likely to be favored in a warming climate by at least two mechanisms. First, their temperature for optimum growth tends to be higher (>25° C), and thus warmer conditions will favor their more rapid accumulation and dominance. Second, a warmer climate can lead to increased phosphorus loadings under increased anoxic stratified conditions, and bloomforming cyanobacteria tend to become increasingly abundant with increasing levels of phosphorus enrichment. Moreover, longer periods of stratification create favorable conditions because cyanobacteria are naturally buoyant and can fix nitrogen in amictic, nutrient-limited epilimnetic conditions (George et al. 1990; de Souza et al. 1998; Jones and Poplawski 1998). Cyanobacteria are inedible to most zooplankton taxa that sustain planktivorous fishes (George et al. 1990; Kangur et al. 2002), so a shift towards cyanobacteria can negatively affect the fish assemblage and fisheries productivity.

The potential effects of climate change on cyanobacteria concentrations have been modelled in large reservoirs of the contiguous U.S. (Chapra et al. 2017). The mean number of days with harmful blooms is expected to increase by 16–23 d in 2050 and 18–39 d in 2090. From a regional perspective, it is predicted that the largest increases in harmful blooms would be in the East and Midwest, with decreases in parts of the West where nutrient concentrations are projected to decline due to changes in loadings caused by decreases in precipitation (Chapra et al. 2017).

3.3.3 Macroinvertebrates

Benthic macroinvertebrates play an important role in the food web of many reservoirs, including the conversion of organic material into food for other organisms, nutrient cycling, and the aeration of sediment (Covich et al. 1999). Climate-driven changes in temperature influence the productive capacity of benthic macroinvertebrates in at least two ways. First, extended bottom hypoxia facilitated by warmer temperatures and stratification could negatively influence benthic macroinvertebrate distribution, production, and recruitment. Second, benthic invertebrates are discouraged by fluctuating water levels, which cause a reduction in species diversity and abundance in nearshore invertebrate communities (Brauns et al. 2008). Most species have little ability to retreat with lowering water levels and become stranded in substrates and desiccate. Species able to migrate with the changing water level (e.g., chironomids) or independent of the substrate (e.g., mobile benthos) may increase in abundance and representation in fluctuating reservoirs. The effects on macroinvertebrates are likely to be more severe in shallow, gently sloping reservoirs than in deep, steep-sided reservoirs.

Sedimentation associated with shifting precipitation patterns is likely to also impact macroinvertebrates. Sedimentation has several direct and indirect effects on benthic macroinvertebrates assemblages, including reduced feeding and growth rates and increased mortality (Donohue and Irvine 2003). Overall, sediment loadings tend to reduce the abundance of benthic invertebrates (Donohue and Irvine 2004). Moreover, alterations to taxonomic composition

can occur (Carew et al. 2007). These alterations frequently include reductions in species richness resulting from the decreases in substrate heterogeneity caused by sedimentation.

3.3.4 Fish assemblages

Habitat modifications prompted by climate change are predicted to have substantial impacts on reservoir fish assemblages and associated recreational fisheries (Hunt et al. 2016; Lynch et al. 2016). Fish species often have broad temperature tolerances, but their population dynamics and community association are sensitive to temperature changes in their environment. Because biochemical reaction rates vary as a function of temperature, and fish body temperature tracks environmental temperature, all aspects of fish physiology, including activity, growth, and reproduction are directly influenced by changes in temperature (Schmidt-Nielsen 1990; Franklin et al. 1995). Thus, increasing global temperatures can affect fish by altering physiological functions such as metabolism, food consumption, growth, and reproductive success. Fish populations faced with changing thermal regimes may increase or decrease in abundance, and experience range expansions or contractions. These shifts will produce changes in fish assemblages that cannot be predicted precisely.

In the U.S. the distribution of freshwater fishes is largely determined by temperature isolines that are principally latitudinal but also altitudinal (Baltz et al. 1987; Moyle and Cech 1988). Freshwater fishes within these clines are often divided into warmwater (physiological optimums >28° C), coolwater (20-28° C), and coldwater (<20° C) (Magnuson et al. 1997). As latitude and altitude increases, fish species are limited by low temperatures that delay the onset of spawning seasons and shorten growing seasons for juveniles, preventing juveniles from attaining enough size in their first year of life to stave off starvation or predation in long winters (Shuter and Post 1990; McCauley and Beitinger 1992; Kling et al. 2003). Conversely, the warm water in lower latitudes and elevations can also restrict species with limitations, such as spawning seasons, that begin too early and last too long (Neal and Noble 2006; Rogers and Allen 2009). There may also be within-drainage latitudinal and altitudinal expansions where fish from reservoirs in lower elevations may now be able to occupy reservoirs further upstream that previously did not have adequate temperature attributes. These invaders, whether indigenous or non-indigenous would vie for space and compete with local species that share similar thermal requirements, habitats, and diets.

Climate warming in the U.S. is projected to produce a northward expansion of warmwater and coolwater fish assemblages including families such centrarchids and percids and a simultaneous distribution contraction of trouts and pikes (Shuter and Post 1990; Jackson and Mandrak 2002). This northern expansion is likely to provide new opportunities for warmwater and coolwater fisheries, but at the expense of coldwater fisheries with substantial uncertainty about fish assemblage structure. Jackson and Mandrak (2002) argue that a northward migration of predators such as smallmouth bass *Micropterus dolomieu* could reduce the diversity of smaller prey-size species. A superficial evaluation could suggest that warming would benefit warmwater fishes in reservoirs, but the potential impacts of warming on habitat and hydrology are difficult to predict with certainty and could impact most species.

Coldwater fish have the best chance of survival in deep, stratified reservoirs in higher latitudes of the contiguous U.S. but are projected to be lost in many regions especially in the mountains of the Northwest, Southwest, and the Northeast through Appalachia. Warming is also projected to have a negative impact on coolwater fish in southern reservoirs, where suitable habitat exists under present conditions. The number of locations in the contiguous U.S. where reservoirs have suitable coldwater and coolwater fish habitat reportedly may decline by up to 45% and 30%, respectively (Stefan et al. 2001). Coolwater fish currently find habitat in seasonally-stratified reservoirs in most of the U.S., but climate warming will introduce summer kills of coolwater species in the southeastern U.S. in reservoirs where suitable habitat existed previously. According to Stefan et al. (2001) the largest negative impact of warming on coldwater fish habitat is projected to occur in medium-depth lakes (13 m maximum depth); the largest negative impact on coolwater fish habitat is projected to occur in shallow lakes (4 m maximum depth).

As precipitation becomes more variable, with more severe wet and dry periods, shifts in reservoir water quality and water levels are projected to change the proportional makeup of reservoir fish assemblages. Small fluctuations in water levels will likely have minimal impacts on freshwater pelagic fishes but could have more serious consequences on littoral species. Littoral fishes inhabit mostly shallow water and represent most of the fish species in reservoirs (Fernando and Holčík 1982). Extreme drought and high-water events would tend to favor open-water species and cause shifts in fish assemblages. In shallow reservoirs and in geographical zones where drought is expected to increase, fish diversity and possibly fish richness may decline, as some species could become rare or locally extinct because of losses in littoral habitat, anoxia induced by interacting high temperature and low water level, and concomitant toxic cyanobacterial blooms. Moreover, variable water levels can substantially increase the variability of year classes and promote "boom and bust" populations and fisheries. Establishment of minimum reservoir water levels suitable for maintaining viable fish assemblages will be important to protect fisheries resources.

Unwanted shifts in population dynamics and fish assemblage composition can also be instigated by eutrophication. Although early stages of eutrophication may enhance fish growth and fishery yield, later stages may force changes in food habits, spatial distribution, and assemblage composition. In Florida lakes, fish biomass increased with eutrophication to a maximum in mesotrophic lakes and fluctuated around the maximum value in hypereutrophic lakes (Kautz 1982). In contrast, fish density increased to a maximum in mesotrophic lakes but declined in hypereutrophic lakes. Piscivores reached maximum biomass and optimum densities in lakes with a total nitrogen concentration of 1,200 ppb and a chlorophyll-a concentration of 11 ppb but suffered adverse effects with further enrichment (Bachmann et al. 1996). Planktivores (Yurk and Ney 1989; Bachmann et al. 1996) and benthivores reportedly increase with eutrophication status (Persson et al. 1991; Jeppesen et al. 2000). Thus, piscivorous fish generally become scarcer in advanced stages of eutrophication, and the ultimate effect, through an increase in zooplankton grazers, is an increase in algae densities (Lathrop et al. 2002; Moss et al. 2011).

3.3.5 Fish invasions

Climate warming can facilitate invasions by non-native species and diminish the ability of native fish assemblages to fend off invasions (Thuiller et al. 2007; Rahel and Olden 2008).

Increases in temperature can raise the probability of invasion and establishment of species originating from southerly latitudes. Because many of the exotic species in the U.S. are from the tropics, increasing temperatures will greatly favor their ability to expand northwards. The northern range limits are typically determined by minimum winter temperatures. Thus, as climate warms, some reservoirs may become suitable for the breeding populations of various non-native species, with often minor but occasionally dramatic influences on native species and fish assemblages (Rahel and Olden 2008). Negative influences may originate from predation, competition, and spread of parasites and diseases (Wrona et al. 2006). The harmful impacts of non-native species can be especially large if they are directed at keystone species or if they substantially change trophic relationships.

Geographic areas with suitable temperatures for warmwater aquaculture and tropical fish culture could expand. For example, optimal temperatures for aquaculture of channel catfish *Ictalurus punctatus* in the southeastern U.S. are projected to move over 200 km northward for every 1° C increase in mean annual air temperature (McCauley and Beitinger 1992). The aquaculture of other warmwater species such as cichlids could also expand to areas currently too cold for outdoor propagation (Peterson et al. 2005). Aquatic organisms occasionally escape captive-breeding facilities and become invasive (e.g., silver carp *Hypophthalmichthys molitrix*, walking catfish *Clarias batrachus*). Non-native species that pose no or minimum threat under current thermal regimes may be able to establish populations and become invasive as climate warms, including many tropical fishes. Climate warming may therefore increase the pool of invasive species by facilitating the spread of fish-culture facilities to new areas.

Altered precipitation and flow regimes resulting from climate warming may influence the pathways by which non-native species are introduced. Overflow of rearing ponds during flood events could promote escapes from aquaculture and tropical fish farm facilities (Padilla and Williams 2004). Changes to the timing and quantity of stream flow may also influence rates of spread of non-native species through river networks. An increase in floods may increase the dispersal capacity of non-native species, such as zebra mussel *Dreissena polymorpha*, whose planktonic larvae are transported through streams (Havel et al. 2005). Increased drought conditions and prolonged low flows associated with climate change may, through various mechanisms, also enhance establishment success of nonnative species (Olden et al. 2006).

3.3.6 Fish growth and recruitment

Warming is expected to enhance growth of warmwater fishes and reduce growth of coldwater fishes, but it is less certain how temperature will affect coolwater species (Portner and Farrell 2008). Increases in temperature encourage growth by providing a longer growing season and by increasing the capacity of fish to digest, at least until metabolic costs become so high that they surpass energy intake (Brett 1979). The temperature at which growth is maximized or begins to decline is species-specific and possibly reservoir-specific, depending ultimately on local habitat conditions and prey availability. According to modelling conducted by Stefan et al. (2001), on average, over the course of the 21st century, good-growth conditions for fish are projected to increase by 37 d/year for coolwater fishes and by 40 d/year for warmwater fishes.

Altered thermal conditions (e.g., faster spring warming, later fall cooling) can affect reservoir fish populations by shifting the timing of reproduction. The extent and direction of these shifts is expected to differ among species and regions of the U.S. depending on whether a species takes its spawning cues from temperature and precipitation that vary annually, or from photoperiod that is invariable and will not be affected by climate change. Most spring-spawning warmwater and coolwater species that take their cues from temperature would be expected to spawn earlier, whereas most fall-spawning coldwater species may be expected to shift spawning until later. Changes in time of spawning, extent of overlap with food availability, and length of growing season (Conover 1990; Garvey et al. 2003) are likely to impact populations in positive and negative ways, many unpredictable.

Warm and wet winters and springs are positively related with recruitment of various fish species in reservoirs (Miranda et al. 1984, 2019; Maceina and Stimpert 1998; Graeb et al. 2010). Thus, climate warming has the potential to influence fish recruitment directly by altering thermal and physical habitat during the spawning season and early development phases (Ludsin et al. 2014). Nevertheless, fish recruitment is influenced by a multiplicity of variables that together regulate the survival and growth of early life stages (Houde 1994; Ludsin et al. 2014). Moreover, most of the evidence for the effect of environmental variables on recruitment comes from single species analyses. Therefore, predictions about the effect of warming climate on fish recruitment are highly uncertain.

4. Toolkit for Coping with Shifting Climate

4.1 Changes are inevitable but we are tooled to deal with them

Most reservoirs in the U.S. were constructed in the 20th century to address existing needs such as flood avoidance, water storage, hydropower generation, and recreation. These reservoirs, their fish habitats, and their fish assemblages have been changing quickly as reservoirs experience relatively rapid aging patterns, albeit at diverse rates (Miranda and Krogman 2015; Pegg et al. 2015). Simultaneously, since the mid-20th century reservoir fisheries have been changing as commercial fishers have mostly vanished and recreational fishers have become dominant. Recreational fisheries have also changed over time as generations of fishers have changed techniques, target species, and leisure versus consumptive behaviors. Over the relatively short history of reservoir management, managers have shifted through several paradigms that have dictated monitoring, management, and research directions (Miranda 1996). Thus, over the short history of reservoir fisheries management, reservoirs and management have not remained static and change is likely to continue with or without climate warming. Hence, reservoir managers have already been coping with change.

However, the changes brought by climate warming are of a larger scale. The extent of the anticipated changes will require that managers readjust approaches toward management, leading to possibly a different operational framework, and yet another shift in the paradigm that dictates how reservoir systems are viewed and managed. Thus, there is a need arising to realign how reservoir fish habitats and fish assemblages are managed, as well as their fisheries, and adapt management to meet the new challenges generated by climate warming.

Adaptation is currently considered the most reasonable approach to cope with forthcoming climate change (Stein et al. 2013; Paukert et al. 2016). The word "adaptation" has been used by ecologists to describe the evolutionary process by which populations change over time in response to their environment. In the context of climate change, adaptation refers to preparing for, coping with, and responding to the impacts of climate change with the goal of minimizing adverse effects (Paukert et al. 2016). Adaptation involves developing strategies to increase the capacity of reservoir ecosystems to absorb disturbances and retain the ability for self-regulation despite alterations (i.e., resilience). A resilient reservoir may be better positioned to serve all or at least some of its purposes under an unpredictable set of conditions generated by climate change (Folke et al. 2010). Resilient reservoirs will continue to function in an altered climate, albeit potentially with a different fish assemblage. However, if climate changes are large a resilient reservoir may be unable to absorb all changes. Thus, managers may also have to allow for and potentially initiate regime shifts to preserve some desired qualities, rather than waiting for irreparable fish habitat damage that causes the collapse of fisheries. Promoting resilience or change may involve tradeoffs that sacrifice historical fishery goals in favor of long-term functionality of the system (Holling 1996; West et al. 2009; Rist and Moen 2013). Management activities for resilience are varied but can be classified into three main classes, including those that address planning, monitoring, and managing of habitats, fish, and anglers (Table 2).

4.2 Planning tools

4.2.1 Clarify goals

Effective reservoir management relies on articulating clear goals, which in turn facilitates the development of relevant management objectives. Goals represent a vision of reservoir habitat conditions that largely reflect ecological, societal, and agency values. These goals are diverse, and include aims such as preserving clean water, maintaining diverse habitats, and controlling erosion. Reservoirs are artificial environments, and ephemeral over a large temporal scale given that they were constructed to last no more than about a century, although clearly some reservoirs will last longer. Considering their artificial nature, the goals for managing aquatic habitats are different than those applied to natural aquatic systems. Although occasionally protection of biodiversity may be a concern if the reservoir serves as temporary refuge for riverine species, or if the reservoir supplies water for maintaining aquatic habitats downstream, the goals of habitat management in reservoirs are more likely to focus on habitat that can provide economic or societal values, such as recreational opportunities, including fisheries. It is important to be clear about why habitat management is important (Barber and Taylor 1990; Slocombe 1998), and what aspects of fish habitat require management attention, before developing strategies to cope with the effects of climate change on habitat.

4.2.2 Assess vulnerabilities

Change in climate may result in irrecoverable loss of fish habitat in some reservoirs. However, depending on various reservoir attributes (e.g., depth, catchment land use, age), reservoirs may differ greatly in their resilience and vulnerability to climatic changes. Because time, funding, and personnel are limited, it is critical for managers to direct resources to reservoirs where the investment has the greatest likelihood of maintaining desired outputs at the least cost. Determining which reservoirs are most vulnerable enables managers to set priorities for management with confidence (Schneider et al. 2007). More vulnerable habitats are likely to experience greater impacts whereas less vulnerable habitats will be less affected or may even benefit from climate change. Distinctions between reservoirs can be made based on a variety of factors estimated to be impacted by climate change or based on characteristics of reservoirs that can make them more or less resilient to climate change. Reservoir vulnerability assessments are a tool that can provide managers answers to questions such as what reservoir characteristics are most likely to be affected by climate change, which fish species may be at risk of population decline or habitat loss, which areas or habitats in the reservoir are most likely to be affected by changes in water temperature and supply, which reservoirs are most at risk, which habitats and reservoirs are high priorities for management to sustain desired fish assemblages, and which habitats may serve as climate change refugia because they are expected to experience the least impact. Moreover, understanding why certain reservoirs are more vulnerable than others provides a basis for developing appropriate management action.

Nevertheless, methods for assessing vulnerability of reservoir habitats to climate change have not yet been established, although some basic models could be developed. There are various databases that describe key physical characteristics of reservoirs nationwide, and there is wide availability of spatial and temporal climate models that permit localized projections on likely changes in temperatures and precipitation at relevant scales. Some of the characteristics most likely to influence the effect of climate change in reservoirs include latitude, elevation, area, depth, catchment area, catchment land use, riparian zone forestation, flushing rate, and water level fluctuations. Existing information could be used to develop regional or nationwide rankings of the relative vulnerability of reservoirs, and to distinguish the specific factors that pose the greatest threats to reservoir fish habitats. The Massachusetts Division of Fisheries and Wildlife recently completed a habitat vulnerability assessment to inform their planning processes (MDFW 2010). The assessment was performed by an expert panel that ranked various aquatic and terrestrial habitats relative to their vulnerability to climate. While the assessment is simplistic, it represents an important first step to identifying vulnerabilities.

4.2.3 Update management goals

As climate shifts, the characteristics of reservoirs will also shift, including changes in habitat properties and biotic community composition. Such long-term realignments will make protecting habitats and species in their original distribution increasingly difficult and in some cases unlikely. As a result, there may be a need to update goals from preserving existing conditions to managing for systems that may differ in habitat or species composition and structure yet continue to function (Cole and Yung 2010). For some reservoirs, particularly the shallow ones that are most

likely to be influenced by climate change, managers may at some point need to revisit the definition of what constitutes desirable habitat conditions and fish assemblages (Hobbs and Cramer 2008; Lemieux et al. 2011).

Climate-driven changes in some reservoirs and geographical regions may be extreme, requiring a shift in management priorities. Some goals may have to be abandoned and new goals established if climate change effects are severe enough. Even with substantial management efforts, some reservoir fisheries may not be able to maintain the desirability that they have in today's climate. For other reservoirs the cost of maintaining a resilient system may far outweigh the returns their fisheries would provide. In such cases, management resources may be better invested elsewhere. An example would be the decision to abandon habitat management in a tributary that provide spawning for a reservoir species (e.g., white bass *Morone chrysops*) because desirable flows no longer occur during the spawning period. If the habitat for the species is becoming unsuitable, it might be best to actively manage a different habitat or for a different species, or for the same habitat and species elsewhere in another reservoir.

4.2.4 Plan for change

Management goals may need to consider a changing future, rather than be grounded exclusively on the current situation. Strategies to achieve goals while accounting for near-term conditions, may also need to take a long-term view of challenges in the horizon in decades ahead. Thus, managers need to be vigilant for opportunities to adjust goals as blurry forecasts about upcoming climatic, ecological, and societal changes come to focus. Most management plans have relatively short 5- to 10 year10-year horizons. Forward-looking plans may require that managers begin incorporating some longer, but softer, 2 to 3 decade goals into current management plans.

4.2.5 Set priorities

Reservoir ecosystems and their fisheries are not equally valuable, nor are they equally vulnerable to adverse impacts from climate change. Setting management priorities can help ensure that the management investment provides the greatest possible benefits. Priorities are best set consulting with a diversity of stakeholders and considering a vulnerabilities assessment. Setting priorities can also involve identifying specific areas within a reservoir that warrant special protection or changes in management owing to their importance to maintaining the fish assemblage in the entire reservoir.

4.2.6 Ensure the needs of fish and fishers are represented

Major shifts in government policy can have major impacts on fish habitats. For example, catchment mismanagement has been identified as a key factor influencing various mechanisms by which reservoir habitats are impacted (Miranda 2017). The effects of climate change need to be considered when land-use policies that might affect reservoir catchments are developed. Policies and initiatives that promote reduced runoff (e.g., conservation tillage, maintenance of buffer strips) are vital to control erosion and sedimentation. It is important that fisheries managers identify reservoir catchments as a specific concern when land-use policies and agricultural guidance are being developed by land-management organizations.

Similarly, water conservation policies can be key to maintaining fish habitats. Policies that establish caps on consumption, freeze urban water footprints, reduce agricultural consumption without reducing yield, encourage more efficient irrigation systems, switch production towards less "thirsty" crops, and others can ultimately determine availability of fish habitat in reservoirs (Postel 2001). Water conservation is one of the most cost effective and efficient ways to address water supply limitations. By using water more efficiently, supplies can be preserved, and fish habitat can be protected. Opportunities for water conservation exist wherever water is used, from domestic consumption to agriculture to energy-related water use. Fishery managers can advocate policy that promote reductions in water demand via changes in water use regulations.

Water level is an important characteristic of reservoir environments. The water level of reservoirs is often controlled by guide curves developed based on historical precipitation levels (Yeh 1985). Guide curves were designed with the assumption of a stationary climate to handle historical conditions, which may no longer be applicable under climate change. Drier summers in many parts of the country will lead to lower reservoir water levels and diminished habitat quality, while wetter winters and springs are likely to produce excessive regular flooding within the reservoir, all of which can lead to degradation of shorelines and nearshore habitats. There is a need for agencies that control water levels to proactively evaluate existing guide curves to adjust to changing conditions and to develop the flexibility needed to adapt to projected changes (Zhang et al. 2017). Past assumptions derived from the historical record about runoff need to be revisited for all reservoirs. Fisheries managers need to have a voice in guide curve updating.

Maintenance and rehabilitation of aging reservoirs is the responsibility of the controlling agency, but funding for maintaining this aging infrastructure is often lacking. As reservoirs age they accumulate sediment and lose storage. Sediment accumulations are often most noticeable at the mouth of tributaries in major embayments. These embayments are key sustainers of reservoir fish assemblages and fisheries. Yet, embayments are often neglected in favor of the mainstem which may support more storage and navigation. The American Society of Civil Engineers estimated that at least US\$64 billion is needed to rehabilitate the nation's non-federal and federal dams, but only about \$6 billion is provided through the Water Infrastructure Improvements for the Nation Act 2016 (ASCE 2017). The lapse in appropriate rehabilitation of impoundments is reportedly driven largely by a lack of political will (ASCE 2017). Advocacy to fund maintenance of our aging reservoir infrastructure needs to be an important element of adaptation to climate change.

Policy action can occur at various levels but is likely to be most beneficial at top levels of government. Organizations that advocate for fishery policy, such as the American Fisheries Society, is likely to be more effectual in shaping widespread change in water management of national scope than local fishery managers working with local dam operators or local soil conservation agencies. However, national organizations also need to adapt to changes. For example, the American Fisheries Society may need a climate change section to coordinate their activities.

Many of the adaptation strategies currently being developed involve changing reservoir operation to meet agricultural, human, and economic needs (Ehsani et al. 2017). The requirements

of fish and fishers may also need to be considered as part of the overall societal adaptation process. The value of local fisheries needs to be addressed in climate-change adaptation plans (Mitchell et al. 2007), even if societal and aesthetic values of a quality environment, healthy fish population, and sustainable recreation are difficult to quantify monetarily. If global climate change leads to significant societal crises, there may be a tendency to view the needs of fishes and the needs of humans as conflicting, rather than complementary.

4.2.7 Prevent arrival of new invasive species

Biological invasions are often irreversible (Rahel and Olden 2008). Given the expansion of invasive exotic species expected with climate warming, adaptation to climate change may need to consider improved policies for management of invasive species. Preventing further introductions is the most effective step towards managing invasive exotic species (Hulme 2006). Many invasion routes have substantial industries supporting them. For example, the aquarium, aquaculture, bait, and commercial shipping industries have in the past been responsible for the spread of exotic species (e.g., fish, mussels, aquatic plants) in North America (Kerr et al. 2005). These routes of introduction imply that more or new policies, or adequate enforcement of existing policies, are needed at the national and state levels to regulate these industries (Peters and Lodge 2009; Barbier et al. 2013).

4.2.8 Incorporate uncertainty

Planning for climate change is extremely difficult because the exercise includes many uncertainties about the physical, chemical, and biological changes that might occur. Whereas some parts of the picture can be predicted with reasonable certainty, many may not, making prediction of the big picture challenging to say the least. Uncertainty can produce lower confidence about the optimal course of action, including whether any action is needed.

To deal with this uncertainty managers may consider four general strategies (Hallegatte 2009). First, apply a no-regrets approach, where the management action can yield benefits even if the projected effect of climate change does not materialize. For example, habitat management activities that help maintain clean water or foster habitat diversity are nearly always a good investment even in the absence of climate change. Second, it is prudent to choose reversible management actions over irreversible options. For example, equipment installed to aerate reservoir hypolimnion or reduce stratification (Miranda 2017) can be removed or turned off at any time if stratification is not as severe as predicted. Similarly, harvest regulations applied to selected piscivores to control expansion of awaited invaders could be rescinded without major impacts. In comparison, if a predator is introduced to avoid angler conflicts that may arise with new regulations, the decision may not be reversible. Third, safety margins to account for uncertainty can often be introduced into habitat management structures during the installation period at small costs relative to making improvements after the project has been finalized. For example, constructed wetlands or pre-dams to control sediment inflows (Miranda 2017) could be oversized, or shoreline riprap to control erosion at unpredicted water levels could be extended up or down cheaper during early planning. Fourth, reduce the time span of management choices or investments. The uncertainty regarding climate conditions increases with time and avoiding longterm commitments could be an option to lower uncertainty and corresponding costs. This strategy may be implemented, for example, when establishing regulatory practices such as relicensing of dams or acquiring conservation easements in riparian zones. In addition to these four general strategies, structured decision models provide alternative quantitative approaches to dealing with uncertainty in climate change. These models are beyond the scope of our review but are examined by Littell et al. (2011) and Nichols et al. (2011).

4.3 Monitoring tools

4.3.1 Document trends

Monitoring is the backbone of management. Reservoir managers routinely rely on monitoring programs to assess spatial and temporal differences in resource status. In the face of climate change, monitoring may be even more essential given there is substantial uncertainty about possible effects. Also, regular monitoring allows detection of changes early and guide management response. Long-term monitoring of impacts of climate change is critical for our ability to adapt (Brekke et al. 2009). Extensive monitoring programs may not be feasible for all attributes of potential interest. A handful of selected attributes such as temperature, dissolved oxygen, water regime, and fish assemblage composition can be priorities in all reservoirs, or in a select group of indicator reservoirs. However, the attributes requiring monitoring are likely to vary among reservoirs or regions depending on the main sources of impacts.

4.3.2 Early detection

Management is often most effective if change is recognized early so that actions can be implemented at initial stages of change. Aspects such as sedimentation, shore erosion, population declines, and invasions are best addressed before they become extensive. Therefore, early detection and rapid response is an important management tool that provides another option when management to prevent negative influences has failed (Davidson et al. 2015). Early detection and rapid response may allow for a more flexible and measured response based on the potential extent of impact and the speed of impact development (e.g., the projected pace of colonization by an invader). Indeed, the thresholds for management action (e.g., control, restoration, eradication, no response) can be identified in advance through monitoring programs designed to detect early stages of change.

4.3.3 Hypothesis-driven monitoring

Monitoring programs are most effective if designed with specific hypotheses in mind (e.g., nutrient levels are stable; species abundance is above a certain level) and with a trigger point that will initiate a policy or a management re-evaluation (Gregory et al. 2006). For instance, using a combination of baseline and historical data, a monitoring program could be set up with pre-defined thresholds for a species' catch rate, growth rate, size structure, or nutrient levels that once transcended, would prompt a re-examination of management goals and objectives. Sampling site selection could focus on those that may best expose biotic and abiotic changes driven by climate change (Brekke at al. 2009), such as the shallow littoral zone of a deep reservoir, a shallow reservoir, or the habitat of a key bellwether species.

4.3.4 Increase flexibility and adaptability

Standardized monitoring programs need to have some flexibility so they can adapt to new unpredicted events and be informed with new knowledge that might develop as habitats and fishes respond to climate change. Monitoring programs may also need to track fisher attitudes and actions because the often-fickle responses of users to changing conditions may dictate how to best implement management actions (Hunt et al. 2016; Paukert et al. 2016). An effective monitoring program can help agencies adapt management programs to address unpredicted challenges.

4.3.5 Coordinate monitoring efforts

Climate change represents a major challenge to reservoir biologists and managers. Managers of other natural resources associated with the reservoir face similar challenges. Monitoring of some waters may need to be intensified to keep up with rapid development prompted by climate change. Sometimes multiple agencies, or branches of the same agency, collect overlapping data on the same reservoir. Coordination across agencies to collect and share complementary data would facilitate expanded monitoring (Quevauviller et al. 2007; Peters et al. 2008).

4.3.6 Enlist volunteers and new technology

Fishers and citizens are often concerned about the quality of reservoir resources and many are willing to participate in monitoring activities. Volunteers and amateurs have added to scientific knowledge for centuries. For example, fields such as astronomy and ornithology encourage volunteers to collect data on stars and bird migrations. In the U.S., many monitoring programs have relied on water chemistry (Kerr et al. 1994; Hoyer et al. 2014), macroinvertebrates (Penrose and Call 1995; Fore et al. 2008), and fish (Cooke et al. 2001; Crandall et al. 2018) data collected by volunteers. Angler data programs can take a variety of forms, from paper-based catch cards, logbooks, and diaries to more technologically advanced online databases and mobile phone applications. The advent of new reporting technologies (e.g., smartphones, text-message-based reporting, angler apps), provide the capacity for real-time data collection and reduces recall bias (Venturelli et al. 2017). Using data collected by volunteers presents various challenges, but if glitches are resolved, volunteers can greatly expand the reach of an agency's monitoring program.

4.4 Managing tools

We list various management strategies potentially applicable to address the need for adapting to climate change, with two qualifications. First, there is always some degree of uncertainty associated with the outcome of any resource management intervention. The results of interventions designed to address climate change are likely to be even less certain, given the uncertainties in future climate. Thus, the efficacy of the strategies is unclear and may depend on

the reservoir. Second, this is not an exhaustive list. Instead, the list may be regarded as a starting line for developing creative alternatives custom-made to local reservoirs and climate conditions.

4.4.1 Partner with outside organizations

Climate change can bring changes too complex and extensive for most reservoir management agencies to address independently. To deal with the vast complexity, management agencies may need to consider joining partnerships across geographic and sociopolitical structures to efficiently use staff and limited fiscal resources. Partnering with catchment, water management, water quality, or non-government conservation organizations can provide the structure needed to plan, fund, and complete required habitat work. Partnerships can provide agencies the capacity to implement activities that may be beyond the exclusive purview of traditional reservoir fish management.

As collaborators, reservoir fish management agencies can contribute skills, experience, and technical expertise about reservoir management to partnerships. Fish managers can be equipped to show the linkages between alterations in the catchment or tributaries and outcomes in the reservoir, and advocate for practices outside the reservoirs that will benefit fish habitat in the reservoir. These efforts can help partners understand ecological processes within the reservoir and thereby develop innovative plans for management outside the reservoir.

As an example, in 1991 the Tennessee Valley Authority (TVA) adopted a reservoiroperating plan that increased the emphasis placed on water quality (Miranda 2017). This plan modified reservoir operation and installed aeration equipment at dams. To prevent these improvements from being negated by nonpoint pollution originating in various sprawling catchments, TVA launched an effort to protect catchments by forging partnerships with governments, businesses, and citizen volunteers. The goal was to ensure that rivers discharging into reservoirs were ecologically healthy. To accomplish this goal without regulatory or enforcement authority, TVA built action teams assigned to sub-basins within the catchment (Poppe et al. 1997). These teams were responsible for assessing resource conditions and building partnerships to address protection and improvement needs. The teams were unique in that they combined the skills of aquatic biologists, environmental engineers, and other water resource professionals with the skills of community specialists and environmental educators. The teams were self-managed and empowered to decide how to focus resources and address protection and improvement needs, allowing for a rapid response to evolving or newly discovered problems and opportunities. By focusing on partnerships, TVA accomplished what they may not have been able to by acting as an independent agency.

4.4.2 Reduce anthropogenic stressors

Reinforcing the resilience of a reservoir system often involves reducing existing pressures on habitats (e.g., sedimentation, eutrophication) and fishes (e.g., overfishing, invasive species) that hinder the ability of reservoir habitats or fish assemblages to withstand stressful climatic events. Thus, this strategy seeks to reduce or remove non-climate stressors to give fishes the maximum flexibility to respond to climate change (Mawdsley et al. 2009). For example, agricultural catchments may require a strong emphasis on managing land use to improve or restore the natural

water retention of the catchment, reduce high flows, and thus retain sediment and nutrients (Furniss et al. 2010). Less intensive land use of riparian zones and protection of filtering zones such as floodplains and wetlands along reservoir edges can also counter the input of sediment and nutrients (Jeppesen et al. 2009). The resilience of fish populations and assemblages could be enhanced by maintaining diverse age structures, modest mortality rates, and steady recruitment by strategically adapting a variety of harvest regulations including a combination of length limits, bag limits, closed seasons, and closed refuge zones, as well as occasional stocking to supplement recruitment as needed (Hansen et al. 2015; Paukert et al. 2016). Conversely, urging harvest of selected species may in some cases help adjust assemblages or help control undesirable invaders.

4.4.3 Protect or restore key reservoir features

Reservoirs have distinctive attributes that are essential to promoting resilience of the overall system. Such key reservoir features could be important focal points for special management protections or actions. For example, some reservoir species require dispersal in and out of tributaries to complete their life history, while others may thrive when there is access to backwaters. In the worst-case scenario, if dispersal is prevented, species may be extirpated locally if they are not able to escape unsuitable thermal, chemical, or hydrological conditions. Thus, if passage is likely to go dry under shifting precipitation patterns, changing water level patterns, or increased sedimentation, pre-emptively maintaining and restoring connectivity to allow fish access to these adjacent habitats is key. If suitable connectivity is hampered, then the responses of fish to climate change may not be realized.

As another example, nearshore zones are key habitats for reservoir fishes, with most of the fish assemblage and fishing activity occurring in this zone (Fernando and Holčík 1982). Targeting improvement of nearshore and riparian zones to maintain a healthy ecotone with diverse substrates, depths, and shade can foster resilience (Furniss et al. 2010). Bank stabilization that prevents erosion during wetting and drying cycles can prevent erosion and homogenization of diverse nearshore environments. These effects could be mitigated by land-use planning to retain mostly intact riparian zones and by planting trees or other vegetation in the riparian areas currently lacking them. Setting aside segments of the riparian zone to protect from extensive development or requesting partners to apply strict guidelines for shoreline zoning can help maintain suitable fish habitat in nearshore areas (Miranda 2017).

4.4.4 Preserve representative habitats

Another management approach to improve resilience involves protecting many habitat types. Representing the diversity of environmental conditions across a locale is a common objective in conservation planning; it has been considered a proxy and hedge for maintaining diverse species assemblages (Faith 2003). A management plan for a large reservoir could include maintaining representation of all available environments. A diversity of environments increases the chances that, regardless of the climatic change that occurs, somewhere in the reservoir system there will be areas that provide refuge or a renewal zone.

4.4.5 Provide refugia

Refugia are habitats less affected by climate change due to factors such as depth, shade, or other key local conditions. Refugia can provide protection from extreme temperature or the effects of extreme low or high precipitation on reservoir fishes. These sites could receive special attention for protection, access, maintenance, restoration, and fish harvesting control. For example, it may be possible to use restoration techniques to reforest steep riparian zones to create shaded thermal refugia for fish species (Raines and Miranda 2016), particularly in north-facing shores that are likely to receive reduced radiation during daylight hours. As another example, excavated pockets along the littoral zone can provide deeper and cooler water in addition to providing habitat diversity. If deep enough, a pocket may have continuous access to groundwater and provide cooler water as well as refuge during droughts (Miranda 2017).

4.4.6 Manage for change

Fisheries agencies have developed management practices based on decades of experience. Fast-tracked climate change may render some long-established management practices ineffective. Reservoir systems, particularly the small and shallow with limited buffering capacity, may experience big enough changes so that strategies suitable to increase ecosystem resilience will no longer be effective, drastically altering habitats and potentially eliminating some or all fisheries in some reservoirs. At that stage, major shifts in reservoir processes and components could be unavoidable, triggering a need to manage for change. Managing for change could mean actively guiding a reservoir through a transformation into a new state. This could involve, for example, nurturing fisheries suited to the new climate habitat conditions because the original fisheries can no longer be supported by the reservoir. In a shallow reservoir with increased water level fluctuations due to shifts in seasonal precipitation, managing for change may mean that pelagial species may be favored over littoral species. Thus, habitat management programs targeting the nearshore, or stocking programs that support recruitment of littoral species, may be shifted to programs that instead manage reservoir stratification problems and stock pelagial species.

Managing for change may also mean applying actions that provide benefits across a range of likely future scenarios (see section 4.2.8). When this is possible, such a tactic would help cope with uncertainties in forthcoming climate and in subsequent environmental and human responses. Focusing on management strategies that are pertinent across multiple future scenarios can provide managers and stakeholders confidence about management strategies and increase the likelihood that strategies will be implemented (Stein et al. 2013).

Managing for change may be complicated by societal expectations. The public in general may expect that agencies will maintain reservoir habitats and fisheries in their current state. They may not recognize the potential impossibility of this goal. Since management will not be able to prevent most changes, but only adjust for change, it will be critical to manage the public's expectations as an integral part of managing for change.

4.4.7 Adjust expectations

Maintaining resilience in reservoir fisheries also requires adjusting the expectations of fishers. Some angler groups are focused on single species and demand that management agencies optimize production of their focus species. These attitudes may require reshaping if we expect to provide gratifying fisheries in the 21st century. In some cases, certain fisheries may be too costly to maintain (DEFRA 2013). Such a change in emphasis on species, or from fisheries that emphasize a single species to fisheries that reflect the ecological capacity of a reservoir environment, is no small challenge for reservoir managers and may take a decade or longer. Management agencies can foster more realistic attitudes through outreach and education designed to promote participation in resource management (e.g., Biggs et al. 2012) and a broader species preference.

4.4.8 Keep vigil on invasive species

Management of spreading invasive species that are established will continue to be essential (Van der Zander and Olden 2008). However, there are species that have already been introduced but have not become problematic, although as climate changes they could (Crooks 2005). Government policy (national and state) and regulations are needed to support risk-reduction measures, including education. However, voluntary codes and education alone will not be effective, but in combination with effective enforcement could lead to risk reduction.

The development of new technology and adaptation of old technology is proving valuable for limiting impacts of invasive species. Barriers of several types are being adopted to exclude invasive fish, both for short-term and long-term protection (e.g., Clarkson 2004; Noatch and Suski 2012; Vetter et al. 2015). Ongoing development of biological controls (Hoddle 2004), and habitat manipulation (Buckley 2008) may improve the efficiency of existing control methods, and enable a broader range of invasive species to be managed. Furthermore, development and adoption of new technologies such as fertility control treatments for feral fish (Jewgenow et al. 2006) or use of population genetics for planning control strategies (Hansen et al. 2008) may improve our ability to reduce the impacts and spread of invasive species.

5. Summary

Climate change has the potential to change fish habitat, fish assemblages, and fisheries in reservoirs across the U.S. through influences on habitat quantity and quality, and by altering species interactions and composition. With the rising temperatures and the shifts in timing and amount of precipitation forecasted in the 21st century, the habitats available to fish will change in many reservoirs. Changes in habitat are expected to alter biological components of reservoir ecosystems that are important to fisheries. The effects, however, will differ greatly across the U.S. given the differences in climate patterns prognosticated among geographical regions, and even within regions given the high diversity of reservoirs relative to altitude, surface area, depth, inflow volume, water residence time, sediment and nutrient influx, and biotic assemblage composition.

Temperature rises could have a variety of effects on reservoirs. First, increased water temperatures are expected to enhance the symptoms of eutrophication through increases in primary production, respiration, and declines in oxygen storage capacity. Warming may increase the potential to produce nuisance algae through nutrient releases from the hypolimnion. Reservoirs may experience a longer stratification period in summer and fall and a single recirculation period. This could enhance eutrophication and lead to oxygen depletion in deep water, eliminating refuges for coolwater or coldwater fish species. Water quality may decline further if anticipated changes in precipitation increase sediment and nutrients entering the reservoir. Seasonal reservoir hydrology and water levels may change as a result of shifts in precipitation. In areas that become drier, lake levels are expected to drop, while in wetter areas levels may rise or become more erratic. Declining reservoir levels could expose littoral habitats, reduce connectivity to surrounding habitats, and reduce habitat availability for fish. In reservoirs where summer inflows decline, dissolved nutrients may linger, increasing productivity and likely contributing to nuisance algal blooms. Fish assemblage composition may shift as a result of climate change. Warmwater fish may expand into northern reservoirs, littoral species may decline in reservoirs with large water level fluctuations, and invasive species may infiltrate native assemblages.

Reservoir managers have already been dealing with shifting conditions as reservoirs have aged rapidly since intense construction in the 20th century. Moreover, managers already have many of the tools needed to address the impacts of climate change in reservoirs. What is most needed is a new perspective on management. The new perspective requires focusing on maintaining ecosystem functionality rather than on retaining composition of desired species. To help reservoir managers adapt to upcoming changes we offer a toolkit organized into three compartments, including planning, monitoring, and managing compartments, equipped with 22 adaptation tools applicable to coping with projected changes in reservoir fish habitats.

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Table 1. Projected consequences of climate-induced changes in temperature and precipitation on physical, chemical, and biological integrity in reservoir environments.

Attribute	Increasing temperature	Changing precipitation	
Physical			
Catchment	Warming can alter land use and vegetative assemblages in the catchment and riparian contour	Increased upstream erosion during floods reduced organic loading from forested landscapes during droughts	
Horizontal habitat connectivity	Rising temperatures may alter some plant/soil communities in floodplains, mostly in upper reaches of reservoirs	Reduced connectivity to tributaries, floodplains, and wetlands due to lower water levels and increased sedimentation	
Storage	Earlier snow melt and ice break up changes timing of water arrival and storage period	Earlier rains, peak flows, and volume transported increases demands for storage; changes in timing of scarce water	
Water residence time	Increased residence time during dry seasons can exacerbate the effects of warmer temperatures and extend stratification	Shorter wet and longer dry seasons may increase residence times and eutrophication	
Water level fluctuations	Increased evapotranspiration may increase rates of drawdown especially in shallow reservoirs	Intermittent severe floods/droughts lead to intense fluctuations; lower levels enhance sediment resuspension, release of sediment-bound nutrients, and reduced DO; loss of habitat diversity as water levels recede into barren contours; encroachment of upland vegetation down to lower reservoir contours	
	Chemical		
Stratification	Higher surface temperatures lead to earlier onset and longer periods of stratification. Simulations estimate warming may lower oxygen in the epilimnion by <2 mg/L, but more in hypolimnion	Onset and extent of stratification are lessened by increased seasonal inflows but exacerbated by reduced inflows in summer and fall	
Water quality	Increases in water temperature and increased biotic respiration reduces dissolved oxygen that controls various chemical reactions that transform water quality	The effects of water pollution, including sediment, nitrogen, phosphorus, and pesticide loadings could be amplified by projected seasonal changes in precipitation	
Eutrophication	Higher temperatures accelerate eutrophication by increasing algal growth, bacterial metabolism, and nutrient cycling rates	Lower inflows increase water residence and reduce nutrient flushing. Where rainfall increases, runoff may hasten nutrient inputs, but this effect may be countered by seasonally higher flushing rates	
Anoxia	Rises in temperature can drop dissolved oxygen and hasten respiration rates of biota. Algal blooms associated with eutrophication may increase diel and seasonal lows and highs	Low flows in summer and fall are expected to intensify anoxia events. With increased anoxia, reservoirs may expect higher incidence of summer and fall fish kills	
Biological			

Aquatic macrophytes	A longer growing season will promote latitudinal and altitudinal expansion and extend the number of days plants experience favorable temperatures for growth. Possibly higher plant density and diversity and altered community composition	Increasingly variable water levels in some regions would tend to prevent aquatic plants but favor moist soil growth in the exposed littoral
Plankton and cyanobacteria	Winter and spring algal phytoplankton biomass could increase. Cyanobacteria could become dominant, and harmful blooms more frequent	Increased residence times in summer and fall when temperatures are favorable for cyanobacteria could worsen blooms
Macroinvertebrates	Increased stratification and hypoxia due to higher temperatures and eutrophication is likely to make large sections of the benthos uninhabitable to macroinvertebrates	Benthic macroinvertebrates are discouraged by water-level fluctuations. Species able to migrate when water levels change (e.g., chironomids) may increase in abundance and representation
Fish assemblages	Cool- and coldwater fishes most impacted, especially in shallow or eutrophic reservoirs, with some populations extirpated. Warmwater taxa such as cyprinids and centrarchids may expand northwards. Changes in vertical occupancy may encourage competition. Smaller and more numerous fishes, fewer piscivores, and reduced top-down control	Drought and high-water events may favor selected species and reshape assemblages. In shallow reservoirs and in geographical zones where drought is expected, diversity and possibly richness may decline, as some species could become rare or locally extinct. Variable water levels could promote "boom and bust" fisheries
Fish invasions	Northward expansions. Winters less of a limiting factor.	Floods and droughts could accelerate rate of invasions through a basin
Fish growth and recruitment	Warming to enhance growth of warmwater fishes and reduce growth of coldwater fishes, but effect less certain on coolwater fishes. Spring-spawning warmwater and coolwater species expected to spawn earlier; fall-spawning coldwater species to spawn later	Wet winters and springs can enhance fish recruitment by giving spawners access to flooded habitat, but this habitat may not be available to juveniles. Predictions about the effect of warming climate on recruitment are highly uncertain

Table 2. Adaptation tools potentially applicable to cope with the consequences of climate-induced changes on reservoir fish habitats.

Adaptation tools	Description		
Planning			
Clarify goals	Goals represent the vision of reservoir habitat conditions shaped by society and agency values. Because reservoirs are artificial environments the goals for managing fish habitats may be different than those applied in natural aquatic systems. It is important to be clear about why habitat management is necessary before developing a plan		
Assess vulnerabilities	Depending on catchment, area, depth, retention time, age, etc. reservoirs differ in their resilience and vulnerability to climatic changes. It is critical to direct resources to reservoirs where investments have the greatest likelihood of maintaining desired outputs at the least cost. Determining which reservoirs or habitats are most vulnerable enables managers to set priorities		
Update goals	Long-term realignments will make protecting habitats and species in their original distribution increasingly difficult, and in some cases unlikely. Some goals may have to be abandoned and new goals established if climate change effects are severe enough. May need to refocus goals from preserving conditions to managing for systems that differ in habitat or species composition and structure yet continue to function		
Plan for change	Strategies to achieve near-term goals need to also consider a long-term view. Thus, management needs to be vigilant for opportunities to adjust near-term goals as blurry forecasts about upcoming climatic, ecological, and societal changes come to focus		
Set priorities	Reservoir ecosystems and fisheries are not equally valuable, nor are they equally vulnerable to adverse impacts from climate change. Setting management priorities can help ensure that the management investment provides the greatest possible benefit		
Ensure the needs of fish and fishers are represented	Shifts in government policy can have big impacts on fish habitats. Policy action can occur at various levels but is likely to be most beneficial at top levels of government. Policies and initiatives about aspects such as land use, water conservation, guide curves, maintenance of aging infrastructure, and transport of exotic species can have long-lasting effects over reservoir fish habitat nationwide and need to be the focus of environmental organizations and professional societies		
Prevent arrival of new invasive species	Regulate importation of species through black-listing; implement early detection and response or eradication protocols to minimize introductions and establishment of non-native species		
Incorporate uncertainty	Planning for climate change includes various uncertainties about the physical, chemical, and biological changes that might occur. Uncertainty can produce lower confidence about the optimal course of action. Various models are listed for incorporating uncertainty into climate change management		
Monitoring			
Document trends	Monitoring is the backbone of management. In the face of climate change, monitoring may be even more essential given the uncertainty about potential effects and actions. Regular monitoring allows detection of changes early, guide management response, and gauge of the effectiveness of management activity		
Early detection	Management is often most effective if change is recognized early so that actions can be implemented at initial stages of change. Early detection also allows for a more flexible and measured response based on the speed of impact development, or potential extent of impact		
Hypothesis-driven monitoring	Monitoring is most effective when applied with specific hypotheses in mind and with a threshold that will trigger a policy or a management reevaluation		
Increase flexibility and adaptability	Design flexibility into monitoring so that programs can be adapted to new unforeseen events and knowledge that might arise as habitat, fish, and users respond to change		

Coordinate monitoring efforts	Coordination across agencies to collect and share complementary data facilitates and expands monitoring	
Enlist volunteers and new technology	Fishers and citizens are often concerned about the quality of reservoir resources and many are willing to participate in monitoring activities. The advent of new reporting technologies (e.g., smartphones, text-messages, angler apps) provide an array of opportunities for data collection	
Managing		
Partner with outside organizations	Climate warming can bring changes too complex and extensive for most reservoir management agencies to address. Partnerships can allow agencies the capacity to implement activities that promote resilient reservoir systems but that are beyond their purview. Partnering with catchment, water management, water quality, or nongovernment conservation organizations can provide the structure needed to plan, fund, and complete needed habitat work	
Reduce anthropogenic stressors	Removing or reducing existing stressors and threats to habitats (e.g., sedimentation, eutrophication) and fishes (e.g., overfishing, invasive competitors) can enhance their resilience to climate change	
Protect or restore key reservoir features	Conserve or restore critical habitats such as connected backwaters, spawning areas in tributaries, spawning and nursery habitats, and nearshore zones	
Preserve representative habitats	Maintain a selection of habitats that reflect habitat diversity in the reservoir (e.g., backwaters, flooded timber, key embayments); maintain or restore connectivity among habitats	
Provide refugia	Establish protected areas with diverse and superior habitat to conserve fish assemblages; increase access to and extent of thermal refugia; provide shade nearshore; maintain diversity of depths in shallow littoral zones	
Manage for change	Managing for change could mean actively managing a transformation into a new state. This could involve nurturing fisheries suited to the expected future habitat conditions because existing conditions are no longer sustainable. It may also mean applying actions that provide benefits across a broad range of likely future scenarios	
Adjust expectations	Maintaining resilience requires adjusting the expectations of fishers. Agencies can foster more realistic attitudes through outreach and education designed to promote participation in resource management and a broader species preference	
Keep vigil on invasive species	Management of spreading invasive species that are already established remains essential. With an expected delay between the time of arrival and time of becoming invasive some species that have already been introduced may yet become invasive. Government policy (national or state) to support risk-reduction, including education, in combination with regulation and enforcement can prevent undesirable expansions	