Hydrobiologia (2015) 745:263–284
DOI 10.1007/s10750-014-2112-1

PRIMARY RESEARCH PAPER

Impacts of land use, climate variability, and management on thermal structure, anoxia, and transparency in hypereutrophic urban water supply reservoirs

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Received: 7 July 2014 / Revised: 6 November 2014 / Accepted: 7 November 2014 / Published online: 28 November 2014

Abstract Reservoir water quality can be compromised by algal production and anoxia, which in turn are impacted by hydrodynamic stability and water temperature. We developed a conceptual model to quantify the dominant controls on stability, anoxia, and transparency using statistical analysis of a long-term (1990–2011) data set for four reservoirs in San Diego, California, each receiving runoff from a watershed with a different level of urban and agricultural land use. We hypothesized that water depth, not air temperature, controlled stability and that anoxia, after correcting for stability, increased and transparency decreased with increasing land use. Depth fluctuated widely interannually and was the dominant control on stability, which in turn controlled transparency in shallow reservoirs. Shallow depth and low stability correlated with low transparency. Transparency decreased with increasing development in the watershed. Water quality deteriorated over time in the reservoirs with the most and, contrary to our hypothesis, least developed watersheds. Deterioration of water quality in the pristine watershed coincided with the introduction of forage fish, which can suppress zooplankton density and translocate phosphorus to the photic zone. The interaction of land use, climate, water level management, basin morphology, and aquatic food webs can deteriorate water quality, even in reservoirs receiving runoff from pristine watersheds.

Keywords Water level fluctuation · Schmidt stability · Eutrophication · Anoxia

Handling editor: Luigi Naselli-Flores

Electronic supplementary material The online version of this article (doi:10.1007/s10750-014-2112-1) contains supplementary material, which is available to authorized users.

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Introduction

Water quality in urban water supply reservoirs can be compromised by high algal production, which can lead to hypoxia and high concentrations of total organic carbon (TOC) in the influent to a water treatment facility (Kraus et al., 2011). TOC increases treatment cost and can generate harmful disinfection byproducts (Falconer, 1999; Richardson, 2003). Two primary categories of controls on algal production and hypoxia are biogeochemical controls, including allochthonous and autochthonous loading of nutrients and organic matter (OM), and thermal and hydrodynamic controls, including the timing, volume, and temperature of inflow; reservoir temperature; and the timing, strength, and duration of thermal stratification.

Allochthonous loading can be impacted by land use and fire in the watershed (Fig. 1). Urban areas export

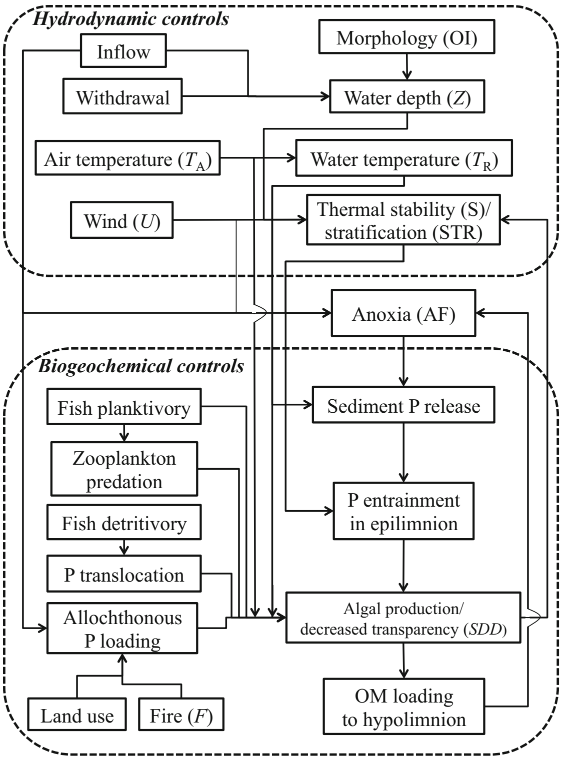

Fig. 1 Conceptual model of controls on development of anoxia in a reservoir

higher quantities of nutrients than natural areas by introducing effluent from wastewater treatment plants (Mclaughlin et al., 2006; Kalscheur et al., 2012) and septic systems (Cunningham et al., 2009), and fertilizer from golf courses (King et al., 2007) and residential lawns (Kelling & Peterson, 1975; Cunningham et al., 2009). Impervious surfaces reduce infiltration, leading to high rates of runoff and pollutant export during storms (Lewis & Grimm, 2007; Tang et al., 2011). Agricultural areas can leach nutrients from excess fertilizer application (Li et al., 2011) or animal waste production (Mcfarland & Hauck, 1999). Fires can increase export of nutrients if ash is transported through overland flow (Lane et al., 2008) or atmospheric deposition (Spencer et al., 2003). A large ratio of watershed area to reservoir surface area is correlated with high anoxia and low transparency in a reservoir (Nõges, 2009).

Autochthonous loading of phosphorus and OM can occur when a legacy of high allochthonous loading is coupled with low dissolved oxygen (DO) in the hypolimnion and in sediment pore water (Fig. 1). Under anoxic conditions, sediment can release soluble reactive phosphorus, iron, ammonia, and manganese to the hypolimnion (Beutel et al., 2007). Liberated phosphorus enhances algal production in the photic zone upon vertical eddy diffusion (Stauffer, 1987), entrainment (Effler et al., 1986), or mixis (Cooke et al., 1993). Dead algae eventually sink into the hypolimnion and sediment, feeding heterotrophic bacteria that consume DO. This positive feedback further degrades water quality by reinforcing a cycle of nutrient supply, production of labile OM, and DO depletion. Reducing allochthonous loading will not necessarily lead to improvements in reservoir water quality if the primary nutrient source is autochthonous (Søndergaard et al., 2003).

Thermal and hydrodynamic controls can impact algal production and anoxia directly and indirectly. Temperature impacts the DO concentration at saturation, with the lowest saturation concentrations of DO at high water temperature. Higher water temperatures are also correlated with increased microbial metabolism (Pettersson, 1998) and release of phosphorus from sediment (Duan et al., 2012). Stratification limits aeration of the hypolimnion, which can lead to anoxia when DO is depleted. Stratification also reduces transport of nutrient-rich water from the hypolimnion into the photic epilimnion, reducing algal production. Breakdown of the thermocline can reduce hypoxia in the hypolimnion, but can also deliver nutrients to the surface and contribute to algal production (Welch & Cooke, 1995). Finally, streamflow carries nutrients and OM to a water body, potentially increasing risk of anoxia and algal production, but below-average streamflow can also correlate with low oxygen concentrations, possibly because streamflow introduces oxygenated water into eutrophic reservoirs with low DO concentrations (Marcé et al., 2010).

In natural lakes, the thermal and hydrodynamic regimes are controlled primarily by weather-related factors, including penetration of solar radiation, sensible heat exchange with the atmosphere, and wind mixing (Boehrer & Schultze, 2008). Warm air temperatures can lead to higher epilimnetic temperatures (Arhonditsis et al., 2004) and higher stability (Jankowski et al., 2006). Earlier onset of stratification can extend the duration of stratification and increase the potential for anoxia (Foley et al., 2012; Wang et al., 2012), leading to concerns about the impact of future climate change on reservoir water quality. High water transparency can increase solar penetration into surface waters and increase thermocline depth and hypolimnetic temperature, reducing stability (Mazumder & Taylor, 1994; Gaiser et al., 2009). Wind can decrease the development of anoxia by mechanically mixing DO across the thermocline (Burns, 1995; Foley et al., 2012) or by turning over the water column to allow circulation and breakdown of the thermocline if the density gradient is weak.

Development of stratification and anoxia often differs in managed reservoirs compared to natural lakes, due in part to larger seasonal and interannual water level fluctuations (WLF) in reservoirs. High amplitude of WLF, as quantified by changes in reservoir mean depth ($\bar{Z}$, calculated as volume, V, divided by surface area, A_0), from drawdown during dry summers in a Mediterranean climate can prematurely destroy stratification and send nutrient-rich water from the hypolimnion to the epilimnion during peak air temperatures in the summer, rather than later in the autumn (Naselli-Flores, 2003; Nowlin et al., 2004). When the water level in a reservoir drops low enough to expose the bed, riparian vegetation may spread onto the exposed sediment, causing biomass to accumulate (Coops et al., 2003). Subsequent die-off of vegetation upon refilling a reservoir can release nutrients and carbon to the reservoir and enhance anoxia (Geraldes & Boavida, 2003). Thus, management practices at a reservoir can increase eutrophication irrespective of allochthonous nutrient addition or climate change (Zohary & Ostrovsky, 2011).

Reservoir morphology also impacts development of stability and both the development and duration of anoxia, so that hydrodynamic and biogeochemical processes differ in deep compared to shallow reservoirs. Nürnberg, (1995) found that the Osgood index (OI; Osgood, 1988), the ratio of mean depth ($\bar{Z}$) to square root of surface area $\left(A_0^{0.5}\right)$, is positively correlated with duration of anoxia because deeper depths (OI > 8) are often coupled with longer stratification. However, OI is negatively correlated with areal and volumetric rates of DO depletion because shallower depths (OI < 6 or 7) correspond to a larger proportional interface between the hypolimnion and sediment, shorter duration of stratification, and longer duration of intensive mixing, all of which increase vertical transport of nutrients (Straškraba et al., 1995) and can contribute to algal production (Cooke et al., 2005).

Fish populations can directly and indirectly impact algal abundance in a reservoir that also functions as a fishery (Schaus et al., 1997). Planktivorous fish can decrease algal abundance through direct predation (Haskell, 1959), but can increase it by grazing zooplankton, which are the primary consumers of algae. Grazing of zooplankton suppresses zooplankton density, which can affect the size, density, and species composition of the phytoplankton community (Henrikson et al., 1980). Detritivory can introduce phosphorus to the photic zone as fish consume phosphorus adsorbed to benthic sediment and then excrete the phosphorus in the epilimnion. In a reservoir that receives little inflow in summer, excretion can be the largest flux of phosphorus (Nowlin et al., 2005). As allochthonous nutrient loading to a reservoir increases in a more heavily developed watershed, so does fish biomass and the supply of phosphorus translocated by excretion (Vanni et al., 2006).

The objective of this study was to identify the main controls on hydrodynamic (stability) and water quality (anoxia and transparency) parameters in reservoirs in a semi-arid Mediterranean climate using statistical analysis of a long-term time series of reservoir water quality, climate, and watershed land use and fire extent data for four reservoirs in San Diego County, California, USA, each of which receives inflow from a watershed with a different level of urban and agricultural land use. Reservoir water quality in San Diego County has been impaired by high algal production (Brown et al., 2000), low DO (White, 1991), high rates of sediment oxygen demand, and sediment release of nutrients and metals (Fast, 1968; Beutel, 2003; Beutel et al., 2007). Objectionable taste and odor have been detected in treated water (Izaguirre et al., 1999).

The major research questions included: Which water quality parameters exhibited trends over the study period and what were the major controls on those trends? Was stability determined primarily by variability in water level or climate, and were anoxia and transparency in turn controlled primarily by stability or by other processes like land use or fire in the watershed? Controlling for stability, were there trends in anoxia or transparency that might indicate changes in allochthonous or autochthonous nutrient loading? Did watersheds with significant expansion of urban development experience the largest increases in anoxia? We hypothesized that (1) water depth, not air temperature, controlled stability, (2) anoxia, after correcting for stability, increased with urban land cover, both over time at a single reservoir and among reservoirs, and (3) algal production, approximated by transparency, during the main production season was controlled by anoxia, stability, and land use. We therefore expected no trends in water quality parameters at reservoirs receiving inflow from minimally disturbed watersheds, and higher anoxia and lower transparency at the most urbanized watershed, both over time and compared to other reservoirs. In the process of answering these questions, we developed a conceptual model for investigating reservoir water quality that controls for the dominant variables affecting stability, anoxia, and transparency.

Methods

Regional setting and study site

The study reservoirs include Barrett Reservoir, Hodges Reservoir, Morena Reservoir, and Sutherland Reservoir (hereafter referred to as Barrett, Hodges, Morena, and Sutherland, respectively; Fig. 2; online resource 1). All are manmade reservoirs that impound surface water for urban use and function as recreational areas for fishing and boating. All inflow to the reservoirs during the study period was generated from runoff in the local watershed, with no imported water from sources outside the county. Barrett and Sutherland have greater depth for a given surface area than Hodges and Morena. All are warm monomictic, but the two shallower reservoirs can be continuous warm polymictic in summer in years when decreased inflow or increased drawdown cause the water column to remain isothermal, inhibiting stratification. All hypolimnia become anoxic when stratified, though DO is depleted at varying rates. Land use in the watersheds includes a heterogeneous mix of urban, agricultural, and natural areas, ranging from relatively pristine (<5% developed for urban and agriculture) to highly developed (38%).

Barrett is located 56 km east of the city of San Diego in a watershed draining 339 km^2. The watershed is the least developed of the study watersheds (95% undeveloped in 2009), as much of the watershed is within Cleveland National Forest. Barrett is the deepest reservoir in the study, with a maximum depth of 42 m, and is the only one to receive water from another source—Morena—in addition to local runoff from its watershed, though Morena is upstream from Barrett and is in the same topographically defined watershed. Barrett is on the United States Environmental Protection Agency list (303[d]) of impaired and threatened waters for color, manganese, perchlorate, total nitrogen, and pH (SWRCB, 2010).

Morena watershed (294 km^2) borders Barrett watershed to the east. The watershed, much of which is also within Cleveland National Forest, is mostly undeveloped (91% undeveloped in 2009), with some rural residential and agricultural areas. Morena is at the highest elevation (926 m asl) and has the largest storage capacity among the study reservoirs. Large fluctuations in water level often interrupt stratification. Morena is 303(d) listed for ammonia as nitrogen, color, manganese, phosphorus, and pH (SWRCB, 2010).

Hodges is located 50 km north of the city of San Diego and 20 km inland from the coast in the largest watershed of the study (641 km^2). Of the study watersheds, Hodges watershed is the most developed (38% developed in 2009), with land uses including urban (10%), rural residential (13%), agriculture (14%), and managed parks (1%). The San Dieguito River drains most of Hodges watershed. Average annual discharge of the river is reduced by 25–31% by groundwater pumping for irrigation upstream of the reservoir (SDPUD, 2011). Hodges is 303(d) listed for color, manganese, mercury, nitrogen, phosphorus, turbidity, and pH (SWRCB, 2010).

Sutherland watershed borders Hodges watershed to the east. The watershed is the smallest (140 km^2) in the study and has the highest areal percentage of agriculture (19%) and little (3%) urban or rural residential area. Sutherland stores the smallest volume among the study reservoirs. Water is transferred from Sutherland to San Vicente Reservoir, where water quality impairments have previously been detected (Izaguirre et al., 1999). Sutherland is 303(d) listed for color, iron, manganese, total nitrogen, and pH (SWRCB, 2010).

Data collection

Temperature, DO, and Secchi disk depth (*SDD*) were sampled at all study reservoirs between 1990 and 2011 by City of San Diego. Vertical profiles of temperature and DO were taken near the deepest location at each reservoir at approximately 1 m depth intervals

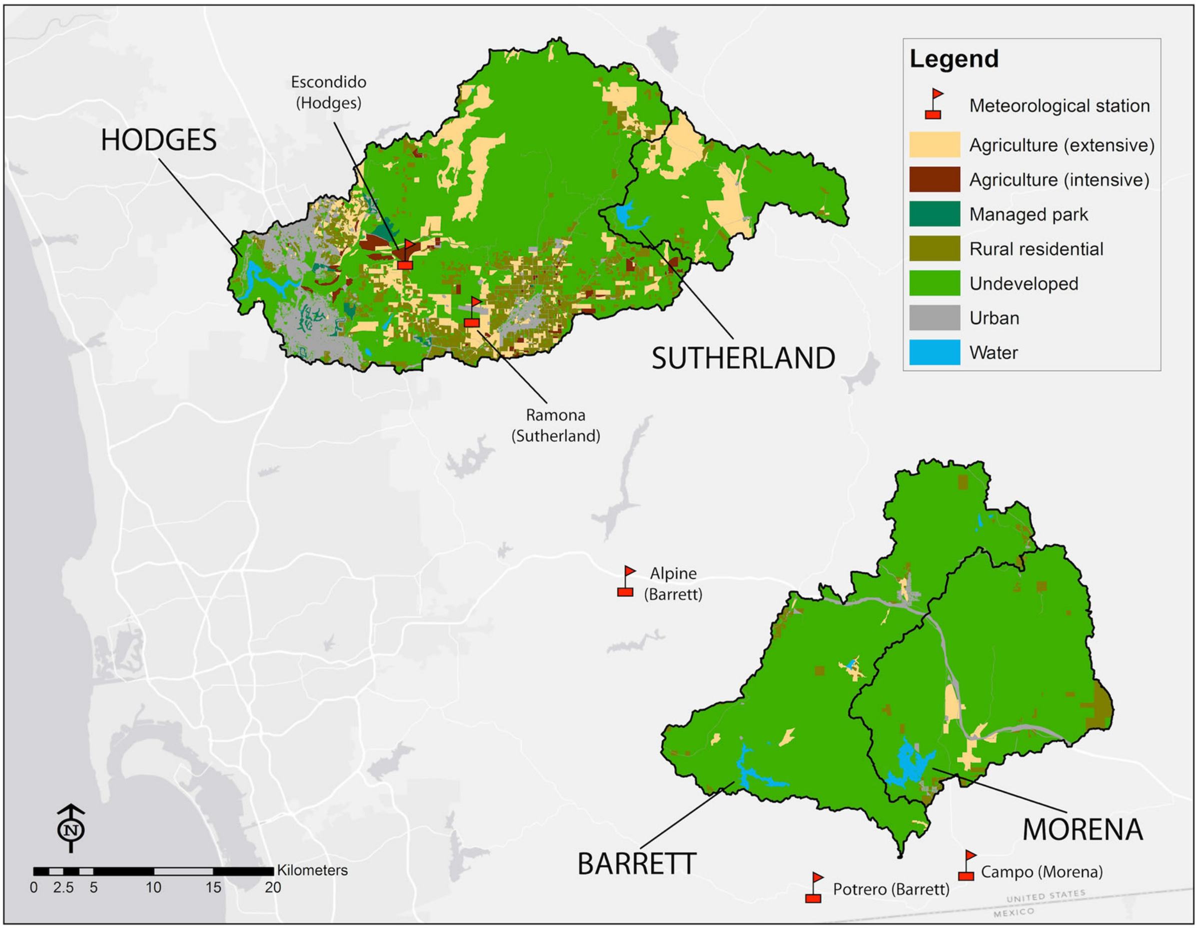

Fig. 2 Map of study reservoirs and land use in their watersheds

throughout the water column. At Barrett and Morena, sampling occurred every 2 weeks, and sometimes weekly, from Jan 1990 to Feb 1993, then approximately monthly until Dec 2011. At Hodges and Sutherland, sampling occurred monthly from Jan 1992 to Dec 2011. Data from the first event of the month was used when multiple observations per month were made. At Morena, there was a gap in data from Jan to Apr 2006, so observations from 2006 were removed from the statistical analysis. Chlorophyll α was sampled between Jul 2001 (Hodges) or Nov 2002 (Barrett, Morena, Sutherland) and Dec 2011. Reservoir depth-area-volume tables were provided by City of San Diego.

Daily air temperature and precipitation data between 1990 and 2011 were obtained for the meteorological station nearest each reservoir from the California Irrigation Management Information System (Hodges; CIMIS, 2013) or from the National Climatic Data Center (Barrett, Morena, Sutherland; NCDC, 2013). Daily wind speed data were obtained for the respective meteorological station or from Western Regional Climate Center (Barrett; WRCC, 2013). Wind data was unavailable at Barrett for 1990 and from 1992 to 1995; at Morena from Jan 1990 to Mar 1998; and at Sutherland from Jan 1992 to Apr 1998.

Land use maps for 1990 and 2009 and land use projections for 2050 were obtained from the San Diego Association of Governments (SANDAG, 2012). The maps are at high spatial (parcel scale) and categorical resolution, with a minimum mapping unit of 10 m^2, and are based on visual interpretation of aerial photography, satellite imagery, and ancillary data, including existing and planned land use, land ownership, and land available for development. For simplicity, we lumped the diverse categories from

SANDAG into urban, which includes high-density residential, industrial, and commercial parcels; rural residential, defined as no more than one dwelling unit per 0.08 km^2; agriculture, which can be further divided into extensive agriculture, which includes field crops, orchards, and vineyards, and intensive agriculture, which includes poultry ranches and dairy farms; managed parks, which includes golf courses, cemeteries, and a zoo; and undeveloped land, which includes open space preserves and vacant land, dominated by chaparral. Land uses were further aggregated into developed areas, which included urban, rural residential, agriculture, and managed parks, and undeveloped areas.

GIS layers of the perimeters of individual fires that burned at least 0.04 km^2 from 1910 to 2010 were obtained from SANDAG (2013). Perimeters are based on GPS points captured on the ground and from aerial imagery. Percentage of watershed area burned in a year was determined by overlaying watershed boundaries onto the time series of fire perimeters.

Data analysis

Reservoir temperature and stability

Volume-weighted temperature was calculated for the whole reservoir (T_R), epilimnion (T_E), and hypolimnion (T_H) for each water temperature profile. The thermocline was defined as the horizontal plane of the maximum temperature gradient, a minimum of 1°C m^{-1}, in the vertical water column (Wetzel, 2001). The lower boundary of the epilimnion was defined as the deepest depth above the thermocline where the temperature gradient between adjacent strata was less than 0.5°C m^{-1} and the upper boundary of the hypolimnion was defined as the shallowest depth below the thermocline where the temperature gradient between adjacent strata was less than 0.5°C m^{-1}.

Strength of stability was quantified using the Schmidt stability index, S (J m^{-2}), which is the minimum amount of work that must be done by wind to return a reservoir to an isothermal state and which is calculated from differences in water density in the water column (Idso, 1973):

$$S = \frac{g}{A_0}\int_0^{Z_m}(Z - Z*)(\rho_Z - \rho*)A_Z \mathrm{d}Z, \qquad (1)$$

where g is acceleration due to gravity (m s^{-2}), A_0 is surface area of the reservoir (m^2), A_Z is reservoir area (m^2) at depth Z (m), ρ_Z is water density (kg m^{-3}) at depth Z, $\rho*$ is mean water density (kg m^{-3}) of the reservoir, and $Z*$ is the depth (m) where the mean water density occurs. The summation is taken over all depths at approximately 1 m intervals, dZ, from the surface to the maximum depth, Z_m.

A reservoir was considered stratified when S exceeded 50 (Morena) or 100 J m^{-2} (Barrett, Hodges, Sutherland). These thresholds were selected because they generally correlated with development and breakdown of a thermocline. Linear interpolation of S between observation dates was used to determine dates of onset of stratification and autumn turnover.

Anoxia

Anoxic conditions were quantified using the Anoxic Factor (AF), which is the number of days in a calendar year for which a sediment area equal to the surface area of a reservoir was overlaid with anoxic water (Nürnberg, 1995). AF was calculated for each year as:

$$\mathrm{AF} = \sum_{i=1}^{n}\frac{t_i a_i}{A_{0i}}, \qquad (2)$$

where t_i is the duration of time period i between successive measurements (d), a_i is the planimetric area of the shallowest anoxic plane (m^2), determined by identifying the shallowest depth where DO was less than 1 mg l^{-1} at the beginning of period i and converting that depth to area using the depth-area relationship for a given reservoir, and A_{0i} is the surface area of the reservoir (m^2) at the beginning of period i. The summation is taken over n in situ observations in each year. Given that AF provides a single value for an entire year, temporal patterns in anoxia within a given year were documented using the anoxic ratio, a_i/A_{0i}, calculated for each measurement date.

Although the rate of hypolimnetic DO depletion at the onset of stratification has been widely used to study development of anoxia in lakes and reservoirs (Beutel et al., 2007; Foley et al., 2012), AF was chosen over the DO depletion rate for several reasons. The oxygen depletion rate determines the rate of developing anoxia but provides no further information about the anoxia after it has been reached (Nürnberg, 2004). Also, AF can be calculated consistently, even if stratification occurs intermittently, such as in reservoirs where water levels may fluctuate widely throughout a year. Most importantly, measurements of DO depletion rates are unreliable when the hypolimnetic DO concentration is below 3 mg l^{-1} at the onset of depletion (Burns, 1995). Volume-weighted hypolimnetic DO concentrations were extremely low at the onset of stratification at Hodges over the study period, ranging from 0.1 to 0.4 mg l^{-1}, with the exception of 1.9 mg l^{-1} in 1992, requiring the use of AF over DO depletion rates.

Secchi disk depth and algal abundance

Ideally, algal production would be monitored directly, but there was only limited data on algal production or chlorophyll α. Instead, Secchi disk depth (*SDD*) is commonly used to estimate algal abundance (Carlson, 1977). However, *SDD* can also be affected by dissolved color (Lind, 1986), detritic particulate OM, or inorganic suspended sediments (Armengol et al., 2003), which can respond to runoff and sediment loading, so the relationship between *SDD* and some index of algal abundance needs to be established for a given study site. There was a statistically significant relationship between chlorophyll α and *SDD* at all study reservoirs, when studied individually and collectively (online resource 2), indicating a significant correlation between algal abundance and *SDD*. We therefore used *SDD* as an indicator of algal abundance, with high *SDD* corresponding to low algal abundance.

Data aggregation

All names and descriptions of variables used in this study are listed in Table 1. Data on water depth, air temperature, wind speed, precipitation, water temperature, stability, and *SDD* were aggregated from daily or monthly observations to annual means for the calendar year (Jan–Dec) to minimize differences among reservoirs caused by different seasonal cycles (online resource 3) and to make data comparable with the annual AF. The calendar year was used to aggregate the data because January was typically the month of minimum water level and minimum stability, so variables over the calendar year correspond to the full cycle of stratification in the late spring and summer and breakdown of stratification in the autumn. The data were also aggregated to means for the unstratified (winter) period, which was defined as Sep–Mar (Morena) or Nov–Mar (Barrett, Hodges, Sutherland).

Statistical analysis and conceptual model

Trends in stability, anoxia, transparency, and controlling variables

Variables were checked for normality both graphically and quantitatively with the Shapiro–Wilk W test for normality (Shapiro & Wilk, 1965). Many variables were not normal, so the statistical significance of a trend was measured using the Kendall rank correlation test (Kendall's τ; Kendall, 1938; Mann, 1945). The magnitude of a trend was given by the Sen slope (Theil, 1950; Sen, 1968), the median slope of all possible pairwise slope estimates, whose statistical significance was given by the significance of Kendall's τ. The Kendall correlation test and Sen slope are both non-parametric and robust against missing data and outliers.

Multiple regression models for stability, anoxia, and transparency

Multiple regression models of stability (S) were determined through forward stepwise variable selection and multiple regression models of anoxia (AF) and transparency (*SDD*) were determined through backward stepwise variable selection. The inclusion of variables for the initial iteration of the selection process was guided by the conceptual model in Fig. 1, typical seasonal patterns in monomictic reservoir dynamics (online resource 3), univariate correlations, and parsimony. Changes in land use or reservoir ecology, like fisheries management, were not included explicitly in the regression models for AF and *SDD* due, for example, to strong temporal autocorrelation in land use variables; instead, the year (YR) was included as an independent variable to capture trends in AF and *SDD* after controlling for other variables. When YR was statistically significant in a regression, we interpreted the trend as caused by some change in either allochthonous or autochthonous loading.

We hypothesized that S in a given calendar year y $\left(S_{[y]}\right)$ was controlled by a combination of mean annual water depth ($\bar{Z}_{[y]}$) and mean annual air temperature $\left(T_{A[y]}\right)$. Regressions were repeated with the addition of

Table 1 Sen slopes of reservoir and meteorological variables showing trends over time (1990–2011)

Variable	Description	Barrett	Hodges	Morena	Sutherland
$\bar{Z}_{[y]}$	Mean water depth (m)	0.03	−0.03	−0.23***	−0.11
$\bar{Z}_{H[y]}$	Hypolimnion mean depth (m)	0.08	−0.04	−0.21**	−0.08
$Z_{\mathrm{th}[y]}$	Depth of thermocline (m)	−0.01	−0.08*	0.10	−0.03
$T_{\mathrm{A[y]}}$	Mean air temperature (°C)	−0.04	−0.07*	−0.0004	−0.003
$T_{\mathrm{Amin[y]}}$	Minimum air temperature (°C)	−0.08*	−0.15**	−0.02	−0.07*
$T_{\mathrm{Amax[y]}}$	Maximum air temperature (°C)	0.01	0.01	0.02	0.03
$U_{\mathrm{[y]}}$	Mean wind speed (m s^{-1})	0.04***	0.002	−0.004	−0.02**
$P_{\mathrm{[y]}}$	Precipitation (mm)	−14.38*	−14.90*	−3.05	1.00
$T_{\mathrm{A[w]}}$	Mean air temperature (winter, °C)	−0.04	−0.09*	−0.01	−0.05
$T_{\mathrm{Amin[w]}}$	Minimum air temperature (winter, °C)	−0.08**	−0.22**	−0.01	−0.09
$T_{\mathrm{Amax[w]}}$	Maximum air temperature (winter, °C)	−0.02	0.01	−0.01	0.02
$U_{\mathrm{[w]}}$	Mean wind speed (winter, m s^{-1})	0.05***	0.004	−0.001	−0.01
$P_{\mathrm{[w]}}$	Precipitation (winter, mm)	−8.93	−9.87	−1.20	2.14
$T_{\mathrm{R[y]}}$	Whole-reservoir temperature (°C)	−0.02	−0.03	0.05**	−0.02
$T_{\mathrm{E[y]}}$	Epilimnetic temperature (°C)	−0.03	−0.06*	0.01	−0.02
$T_{\mathrm{H[y]}}$	Hypolimnetic temperature (°C)	0.01	−0.03	0.20*	−0.04
$T_{\mathrm{R[w]}}$	Whole-reservoir temperature (winter, °C)	0.01	−0.01	0.01	−0.01
$\mathrm{S_{[y]}}$	Mean Schmidt stability (J m^{-2})	1.63	−2.91	−14.04***	−3.58
$\mathrm{S_{max[y]}}$	Maximum Schmidt stability (J m^{-2})	0.12	−4.75	−33.61***	−15.92
$\mathrm{S_{[w]}}$	Mean Schmidt stability (winter, J m^{-2})	1.26	−0.73	−6.96***	−0.98
$\mathrm{STR_{on[y]}}$	Onset of stratification (doy)	−0.50	0.26	3.29**	1.17
$\mathrm{STR_{dur[y]}}$	Duration of stratification (d y^{-1})	0.64	−1.05	−12.11***	−0.31
$\mathrm{AF_{[y]}}$	Anoxic Factor (d y^{-1})	3.37**	2.05**	−5.44**	0.46
$SDD_{\mathrm{[y]}}$	Secchi disk depth (m)	−0.05*	−0.003	−0.06	−0.01
$SDD_{\mathrm{[w]}}$	Secchi disk depth (winter, m)	−0.04**	−0.002	−0.08*	−0.02
$F_{\mathrm{[y]}}$	Watershed area burned (%)	0.00	−0.01*	0.00	0.00

Variables are means aggregated by calendar year (Jan–Dec, subscript y) or winter unstratified period (Nov–Mar, subscript w). Significance was determined by Kendall's τ. Data for years when a reservoir did not stratify were excluded from the analysis

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

less commonly significant variables, including mean annual wind speed $\left(U_{[\mathrm{y}]}\right)$ and mean annual SDD $\left(SDD_{[\mathrm{y}]}\right)$:

$$S_{[\mathrm{y}]} = f\left(\bar{Z}_{[\mathrm{y}]}, T_{\mathrm{A[y]}}\right) \tag{3a}$$

$$S_{[\mathrm{y}]} = f\left(\bar{Z}_{[\mathrm{y}]}, T_{\mathrm{A[y]}}, U_{[\mathrm{y}]}, \mathrm{SDD}_{[\mathrm{y}]}\right), \tag{3b}$$

where the subscript y indicates the mean of the variable for the calendar year. Regressions were repeated with the date of onset and duration of stratification as dependent variables.

We hypothesized that AF in a given calendar year $\left(\mathrm{AF}_{[\mathrm{y}]}\right)$ was controlled by a combination of the duration of stratification $\left(\mathrm{STR}_{\mathrm{dur[y]}}\right)$, stability $\left(\mathrm{S}_{[\mathrm{y}]}\right)$, and air and water temperature $\left(T_{\mathrm{A[y]}}, T_{\mathrm{R[y]}}, T_{\mathrm{E[y]}}, T_{\mathrm{H[y]}}\right)$ during the same calendar year and by OM input from the winter or year prior to the onset of stratification. Loading of OM was allochthonous, represented by the fraction of the watershed burned $\left(F_{[\mathrm{y}-1]}\right)$ and precipitation $\left(P_{[\mathrm{w,y}-1]}\right)$, and autochthonous, represented by algal production $\left(SDD_{[\mathrm{w,y}-1]}\right)$:

$$\mathrm{AF}_{[y]} = f\left(\mathrm{STR}_{\mathrm{dur}[y]}, S_{[y]}, T_{\mathrm{A}[y]}, T_{\mathrm{R}[y]}, T_{\mathrm{E}[y]}, T_{\mathrm{H}[y]}, F_{[y-1]}, P_{[\mathrm{w},\, y-1]}, \mathrm{SDD}_{[\mathrm{w},\, y-1]}, \mathrm{YR}_{[y]}\right), \quad (4)$$

where the subscript "w, y−1" indicates the mean of the variable in the winter months (Nov–Mar) prior to and at the beginning of that calendar year. For example, in the year 2000, $\mathrm{AF}_{[y]}$ is the Anoxic Factor calculated for Jan 2000 through Dec 2000, $T_{\mathrm{A}[y]}$ is mean air temperature for Jan 2000 through Dec 2000, $F_{[y-1]}$ is total watershed area burned for Jan 1999 through Dec 1999, and $SDD_{[w,\ y-1]}$ is mean Secchi disk depth for the winter, Nov 1999 through Mar 2000. We used *SDD* measurements averaged over the winter rather than over the calendar year because *SDD* was at its maximum and algal abundance was minimum during the summer period of stratification due to inhibited nutrient transport across the thermocline (online resource 3). Following the breakdown of stratification in the autumn and early winter, *SDD* decreased rapidly as algal production increased due to mixing of nutrient-rich water from the hypolimion into the photic epilimnion. This equation assumes that algal production later in the year (Sep–Dec) did not contribute to the development of anoxia in that calendar year (Jan–Dec), given that anoxia was maximal during the summer and that annual AF should be controlled by algal production and OM input prior to the development of maximum anoxia (online resource 3).

Finally, algal abundance, approximated by $SDD_{[w]}$, during the main production season in winter should then be controlled by winter stability ($S_{[w]}$), winter air and water temperature $\left(T_{\mathrm{A}[w]}\text{ and }T_{\mathrm{R}[w]}\right)$, and nutrient input to the epilimnion in winter or the calendar year prior to the winter. Loading of nutrients was allochthonous, represented by the fraction of the watershed burned $\left(F_{[y]}\right)$ and precipitation $\left(P_{[w]}\right)$, and autochthonous, represented by the duration of stratification $\left(\mathrm{STR}_{\mathrm{dur}[y]}\right)$ and anoxia $\left(\mathrm{AF}_{[y]}\right)$:

$$\mathrm{SDD}_{[w]} = f\left(S_{[w]}, T_{\mathrm{A}[w]}, T_{\mathrm{R}[w]}, F_{[y]}, P_{[w]}, \mathrm{STR}_{\mathrm{dur}[y]}, \mathrm{AF}_{[y]}, \mathrm{YR}_{[y]}\right), \quad (5)$$

where the subscript w indicates the mean in the winter months (Nov–Dec) at the end of the calendar year y and winter months (Jan–Mar) at the beginning of the next calendar year, y + 1. Stratification and anoxia both represent soluble phosphorus released from sediment into the hypolimnion, though they are distinct from each other in this context. $SDD_{[w]}$ should decrease (and algal production increase) when $S_{[w]}$ is low, due to mixing of nutrient-rich hypolimnetic waters into the epilimnion.

Backward selection was an iterative process of deleting the least significant term in a maximal model until remaining terms were significant ($\alpha = 0.05$; Crawley, 2007). The model that explained the most variance (R^2) for a given dependent variable was selected as the final minimal adequate model. The relative contribution to R^2 from each term, alone and in combination with others, in a model was based on sequentially determined R^2s, which depend on the order in which terms were entered into a regression. To control for the sequence of addition, the unique contribution to R^2 for an explanatory variable was given by the Lindeman, Merenda, and Gold (LMG) statistic (Lindeman et al., 1980; Grömping, 2006). The statistic can be interpreted as the average squared semi-partial correlation coefficient for a regressor, which is determined as the average of all possible permutational orderings of that regressor within the set of all regressors. The variance inflation factor of each independent variable in all regression models was below five, indicating minimal problems with multicollinearity (Draper & Smith, 1981).

Results

Land use and fire history

Urban and rural residential land use expanded in all study watersheds between 1990 and 2009, largely replacing agriculture, rather than natural vegetation, leaving total developed area stable in the most developed watersheds (Hodges and Sutherland; online resource 4). Hodges watershed had the most urban and rural residential area (10 and 13% of watershed area, respectively) and experienced the largest expansion in both (1 and 5% of watershed area, respectively). Rural residential land use is forecast to increase by factors of 3 (Barrett) to 14 (Sutherland) and will be the dominant land use after open space by 2050 in all watersheds. Urban land use is also forecast to expand across all watersheds.

Fires occurred regularly in all watersheds, burning in 34–63 years from 1910 to 2010. Mean percentage of watershed area burned in a burn year was similar

(3.1–3.9%) across all watersheds, though there was variation in burned area during large burn years. The largest percentage of watershed area burned over the study period was in Hodges watershed, followed by Sutherland, Barrett, and Morena watersheds (online resource 4).

Reservoir water level fluctuations

Intra- and inter-annual WLF were large at all study reservoirs over the study period (Fig. 3; Table 2). Fluctuations in maximum depth were largest at Sutherland, which experienced a maximum intra-annual range of 21 m in 1998 and an interannual range of 26 m (14.6–40.6 m), followed by Morena, Barrett, and Hodges. Water level decreased significantly and monotonically over time at Morena, by an average of 0.9 m y^{-1} over the study period (Table 1). The intra- and inter-annual WLF observed at the study reservoirs were comparable to and generally on the upper end of the range observed in other managed reservoirs (Table 2).

Climate and water temperature

Mean annual minimum air temperature in the calendar year ($T_{\mathrm{Amin[y]}}$) decreased significantly in three of four watersheds and mean annual minimum air temperature in winter $\left(T_{\mathrm{Amin[w]}}\right)$ decreased significantly in two (Table 1). The trend in mean air temperature in the calendar year and in winter was negative for all watersheds, but was statistically significant in only one (Hodges) of them. Mean annual wind speed in the calendar year increased in one watershed (Barrett) and decreased weakly in another (Sutherland).

The water temperature of the whole reservoir $\left(T_{\mathrm{R[y]}}\right)$ and of the hypolimnion $\left(T_{\mathrm{H[y]}}\right)$ increased significantly over the study period only at Morena, likely due to the decrease in water depth over the study period. $T_{\mathrm{R[y]}}$ and epilimnetic temperature $\left(T_{\mathrm{E[y]}}\right)$ had negative trends at Barrett, Hodges, and Sutherland, but the trend in $T_{\mathrm{E[y]}}$ was statistically significant only at Hodges.

Stability and stratification

Stability $\left(\mathrm{S}_{[y]}\right)$ varied intra- and inter-annually at all study reservoirs over the study period (Fig. 3). The two deeper reservoirs (Barrett and Sutherland) were more stable than the two shallower reservoirs (Hodges and Morena; Table 3). Stability decreased significantly at Morena over the study period, likely due to the decrease in water depth, and stability decreased less significantly at Hodges ($P = 0.06$).

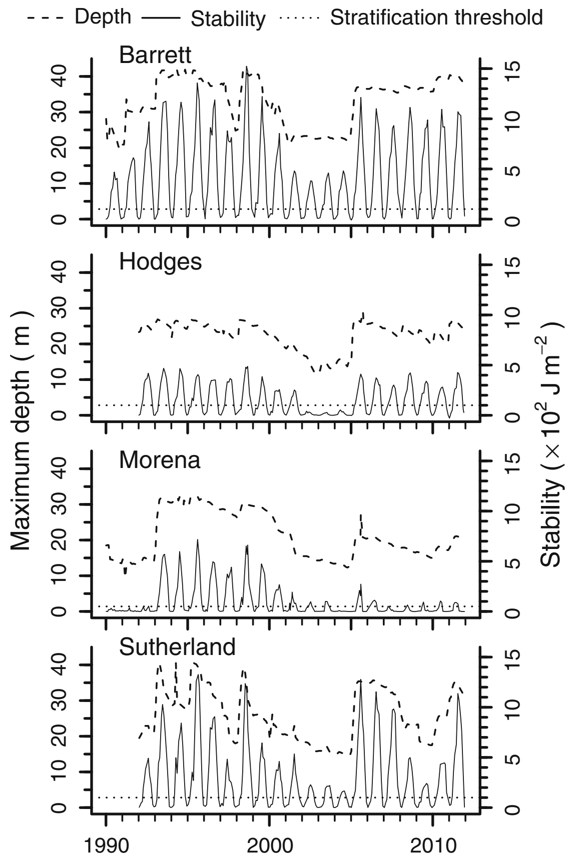

Fig. 3 Time series of maximum depth and Schmidt stability at study reservoirs from 1990 to 2011

Stability was controlled primarily by water depth $\left(\bar{Z}_{[y]}\right)$, which explained 80–97% of the variance in stability at all study reservoirs (Fig. 4; Table 4; online resource 5–8). Air temperature $\left(T_{\mathrm{A[y]}}\right)$ was a statistically significant but minor predictor variable at three reservoirs, increasing R^2 by 0.01, 0.16, and 0.01 at Barrett, Hodges, and Sutherland, respectively. In the multiple regression with more independent variables (Eq. 3b), wind speed and *SDD* were not statistically significant predictors of stability at any reservoir.

Stratification patterns closely resembled those of stability. Onset of stratification was earliest and duration of stratification was longest at Barrett,

Table 2 Water level fluctuations in managed and natural lakes

	Date range	Intra-annual amplitude, avg ± SD (max) (m)	Inter-annual amplitude, max (m)	Reference
Managed lake, location				
Shasta, USA	1990–2009	18.4	47.0	Zohary & Ostrovsky (2011)
Sutherland, USA	1992–2011	7.3 ± 5.9 (21.0)	26.0	This study
Mead, USA	1992–2004	–	25.0[a]	LaBounty & Burns (2005)
Burragorang, Australia	1988–2007	–	~25.0	Vilhena et al. (2010)
Morena, USA	1990–2011	3.9 ± 3.8 (14.3)	22.8	This study
Barrett, USA	1990–2011	5.2 ± 5.1 (16.8)	22.4	This study
Liuxihe, China	1959–2009	–	22.0	Wang et al. (2012)
Arancio, Italy	1990–2009	3.3	20.5	Zohary & Ostrovsky (2011)
Hodges, USA	1992–2011	3.5 ± 2.6 (13.7)	17.2	This study
Hartbeespoort, South Africa	1990–2009	1.5	~10.0	Zohary & Ostrovsky (2011)
Serra Serrada, Portugal	1995–2001	–	8.0–10.0	Geraldes & Boavida (2003)
Sooke, Canada	2000–2001	~6.3	~6.3	Nowlin et al. (2004)
Kinneret, Israel	1967–2007	–	6.0	Rimmer et al. (2011)
Natural lake, location				
Constance, Germany	1950–2010	1.5 ± 0.4 (2.5)	3.0	Wantzen et al. (2008)[b]
Van, Turkey	1944–1974	0.5 ± 0.2 (1.0)	2.2	Kadioglu et al. (1997)[b]
16 Canadian lakes[c]	1980–2003	0.3 ± 0.2 (1.3)	~2.0	White et al. (2008)[b]
Kinneret, Israel	1100–1932	1.1 ± 0.5 (1.5)	1.8	Hambright et al. (2004)
Biwa, Japan	1990–2009	0.8 ± 0.3 (1.4)	1.5	Japan Min. of Infrastructure, Transport, and Tourism[b]
Erie, USA	1900–2009	–	~1.5	Bouffard et al. (2013)
Shawnigan, Canada	2000–2001	0.5 (0.5)	0.5	Nowlin et al. 2004

[a] Calculated from mean annual water elevation

[b] See table in Zohary & Ostrovsky (2011)

[c] Laurentian Great Lakes region

followed by Sutherland, Hodges, and Morena (Table 3). Onset of stratification occurred as early as February 6 at Barrett in 1996 and as late as May 23 at Morena in 2008. At Morena onset of stratification occurred significantly later over time and duration of stratification decreased significantly over time, also likely due to the decrease in water depth over the study period.

As with stability, duration of stratification ($STR_{dur[y]}$) was controlled primarily by water depth ($\bar{Z}$; Fig. 5; Table 4; online resource 5–8); air temperature was statistically significant only at Hodges. In the multiple regression with more independent variables, wind speed and *SDD* were not statistically significant predictors of duration of stratification at any reservoir. Overall, water depth was the dominant control on stability, with air temperature playing a secondary and minor role. Low water levels led to low stability and inhibited stratification in some years at the two shallower reservoirs, Hodges (2002–2004) and Morena (1990–1992, 2004).

Anoxia and transparency

All study reservoirs were hypereutrophic over the study period, using the criterion of Nürnberg (2004; $AF_{[y]} > 60$ d y^{-1}; Fig. 6; Table 3). $AF_{[y]}$ ranged from 5.3 at Morena in 2007 to 239.4 at Barrett in 2009 and was lower in years when a reservoir did not stratify. $AF_{[y]}$ increased significantly over time at Barrett, by an average of 3.4 d y^{-1} over the study period, and at Hodges (in years when Hodges stratified), by an average of 2.1 d y^{-1} over the study period (Table 1). The trend analysis was supported by the $AF_{[y]}$

Table 3 Mean annual (Jan–Dec, except *SDD*) values of thermal and oxic characteristics of study reservoirs from 1990 to 2011

Reservoir	T_R (°C)	T_E (°C)	T_H (°C)	S (J m^{-2})	S_{max} (J m^{-2})	STR_{on} (doy)	STR_{dur} (d y^{-1})	Z_{th} (m)	AF (d y^{-1})	$SDD_{[y]}$ (m)	$SDD_{[w]}$ (m)
Barrett	15.0	21.0	11.6	411	942	63	266	7.2	161	1.8	1.6
$Hodges_{ST}$	17.6	23.1	14.1	174	377	85	220	6.5	157	1.0	0.9
$Hodges_{NS}$	18.7	–	–	13	41	–	–	–	36	0.7	0.7
$Morena_{ST}$	15.3	20.5	13.0	106	311	101	154	8.5	60	1.7	1.7
$Morena_{NS}$	15.6	–	–	8	32	–	–	–	11	1.0	0.9
Sutherland	15.2	22.4	11.3	300	715	83	229	5.8	149	1.2	1.1

Volume-weighted temperature of the whole reservoir (T_R), epilimnion (T_E), and hypolimnion (T_H); mean Schmidt stability (S); maximum Schmidt stability (S_{max}); onset of stratification (STR_{on}); duration of stratification (STR_{dur}); depth of thermocline (Z_{th}); Anoxic Factor (AF); and Secchi disk depth for Jan–Dec ($SDD_{[y]}$) and for the unstratified period ($SDD_{[w]}$). Separate means are reported for Hodges and Morena during years when they stratified (ST) and years when they did not stratify (NS)

Note T test results indicate that mean $SDD_{[y]}$ over the study period was significantly ($P < 0.01$) different at Morena in years when it stratified compared to in years when it did not stratify

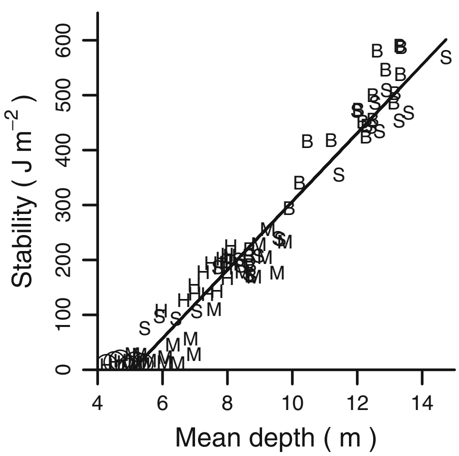

Fig. 4 Relationship between mean annual (Jan–Dec) mean water depth and mean annual (Jan–Dec) Schmidt stability. The equation ($y = -316.502 + 62.291 \times x$) gives an Adj. $R^2 = 0.94$ ($P < 0.001$). Points in *circles* indicate years when a reservoir did not stratify

regressions, in which the time variable (YR) was statistically significant for Barrett and Hodges (Table 5). The correlation between AF and year at Hodges and Barrett, after controlling for stability, duration of stratification, depth of the hypolimnion, and air and water temperature (Table 5), suggests that other processes are responsible for changing AF over time, including changes in algal production, allochthonous or autochthonous loading, and/or other unaccounted for processes, rather than due to changes in hydrodynamics (Fig. 1). $AF_{[y]}$ decreased significantly at Morena (in years when Morena stratified) over the study period.

AF was controlled by stability when comparing all study reservoirs together (online resource 9). AF increased with stability among the reservoirs and was highest at the most stable and deepest reservoir (Barrett). However, when reservoirs were studied individually, stability and duration of stratification were not statistically significant controls on AF at two of the four reservoirs (Table 5), and some reservoirs (Hodges) showed higher $AF_{[y]}$ than other reservoirs (Morena) for a given stability (online resource 9). One reservoir (Barrett) showed a negative relationship between AF and stability in the multiple regression (Table 5), which may be due to the inclusion of other variables in the regression that create artifactual correlations. The scatter in the stability-AF relationship (online resource 9) was explained in large part by $SDD_{[w,\ y-1]}$ as indicated by a plot of $SDD_{[w,\ y-1]}$ versus the residuals of the $S_{[y]}$-$AF_{[y]}$ relationship (online resource 10) and by regression results (Table 5), suggesting that high algal abundance in winter results in a higher $AF_{[y]}$ in the following year. AF was unrelated to land use in the watershed; the highest AF occurred at the reservoir (Barrett) whose watershed had the least amount of development.

Air and/or water temperatures were significant controls on anoxia at all reservoirs in the initial regressions (data not shown). However, for Barrett, the sign for the T_R coefficient was negative whereas the sign for the T_H coefficient was positive. This may be a spurious result, given the positive and significant correlation between T_R and T_H (online resource 5). The negative sign for the T_R coefficient may be due to

Table 4 Regression results for mean annual (Jan–Dec) reservoir hydrodynamic characteristics as functions of reservoir mean annual mean depth ($\bar{Z}$) and mean annual mean air temperature (T_A) at Barrett (BA), Hodges (HO), Morena (MO), and Sutherland (SU)

Response variable	Reservoir	β		LMG		R^2	RMSE
		$\bar{Z}$	T_A	$\bar{Z}$	T_A		
Whole-reservoir water temperature (T_R)	BA	Ns	0.51***	0.01	0.51	0.52***	0.38
	HO	−0.46***	0.49***	0.56	0.25	0.80***	0.26
	MO	−0.18**	0.51*	0.29	0.20	0.49**	0.40
	SU	−0.14**	Ns	0.36	0.08	0.44**	0.48
Schmidt stability (S)	BA	77.2***	24.5*	0.94	0.01	0.95***	30.7
	HO	47.9***	11.4*	0.80	0.16	0.95***	14.2
	MO	50.2***	Ns	0.89	0.00	0.89***	28.8
	SU	57.3***	−25.5*	0.97	0.01	0.97***	27.1
Duration of stratification (STR_{dur})	BA	14.9***	Ns	0.73	0.01	0.74***	15.0
	HO	18.9**	10.4*	0.37	0.28	0.66***	12.1
	MO	45.6***	Ns	0.72	0.01	0.73***	43.6
	SU	15.0***	Ns	0.85	0.00	0.85***	17.4
Depth of thermocline (Z_{th})	BA	0.34**	Ns	0.34	0.02	0.36*	0.78
	HO	Ns	Ns	0.22	0.03	Ns	Ns
	MO	Ns	Ns	0.01	0.08	Ns	Ns
	SU	0.26***	Ns	0.55	0.06	0.61***	0.58

The β is the regression parameter value and LMG is the relative contribution of each variable to the final R^2 (Grömping, 2006). Data for years when a reservoir did not stratify were included in the analysis

Ns $P > 0.05$

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

a negative and significant correlation between T_R and the ratio of the hypolimnion to epilimnion volume. In a deep reservoir, such as Barrett, oxygen depletion occurs primarily in the hypolimnion, rather than in sediment (Charlton, 1980; Bouffard et al., 2013). Therefore, we substituted T_R with the mean hypolimnetic depth $\left(\bar{Z}_{H[y]}\right)$ in the initial iteration of the variable selection process and then found positive and significant correlations between AF and hypolimnion size (depth and surface area) at Barrett (online resource 5).

$SDD_{[y]}$ and $SDD_{[w]}$ were smallest at Hodges, indicating that Hodges was the least transparent and the most eutrophic of the study reservoirs. $SDD_{[y]}$ decreased significantly over time at Barrett, by an average of 5 cm y^{-1} over the study period, and $SDD_{[w]}$ decreased significantly over time at Morena, by an average of 8 cm y^{-1} over the study period, although mean $SDD_{[y]}$ over the study period was largest at Barrett and mean $SDD_{[w]}$ over the study period was largest at Morena (Table 3). $SDD_{[w]}$ also decreased significantly over time at Barrett, by an average of 4 cm y^{-1} over the study period, and the trend analysis was supported by multiple regression results (Table 5). $SDD_{[y]}$ was smaller in years when a reservoir did not stratify.

In contrast to AF, mean *SDD* over the study period was significantly related to land use (in 2009) and decreased with increasing development in the watershed draining to each reservoir (online resource 11). Burned fraction of the watershed and precipitation were significant controls on *SDD* only at Sutherland. Stability was not an important control on *SDD* when comparing across all reservoirs, but was an important control on interannual variability in *SDD* at the shallower reservoirs (Hodges and Morena), where $SDD_{[w]}$ was larger in years with higher winter stability ($S_{[w]}$; Table 5) and $SDD_{[y]}$ was smaller in years when a reservoir did not stratify (Table 3). This is in

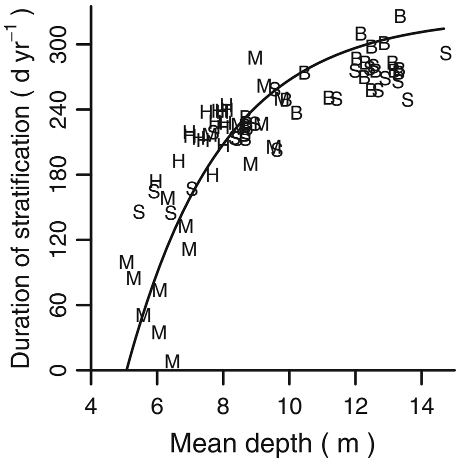

Fig. 5 Relationship between mean annual (Jan–Dec) mean water depth and annual duration of stratification with non-linear regression model, given by the equation, $y = 326\left(1 - e^{-0.3479(x-5.075)}\right)$, where e is the base of the natural logarithm. The lower limit of x is 5.075, the minimum observed mean annual mean water depth (m), and the upper limit of y is 326, the maximum observed duration of stratification (d y^{-1})

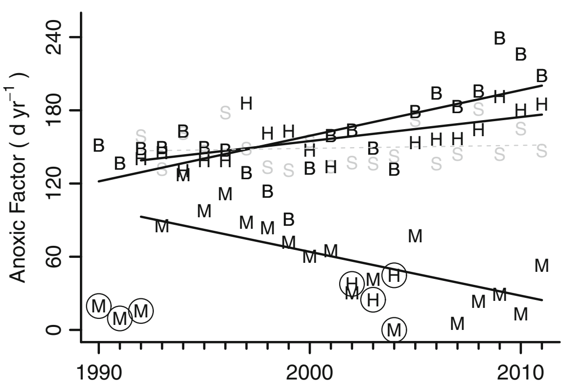

Fig. 6 Time series of the Anoxic Factor at study reservoirs from 1990 to 2011. *Solid black regression lines* indicate a significant trend in Kendall's τ (α = 0.05). There was no trend at Sutherland (*grey dashed line*). Points in *circles* indicate years when a reservoir did not stratify and which were omitted when calculating the regressions

agreement with our conceptual model, as higher stability prevents nutrients in the hypolimnion from mixing into the epilimnion in shallow reservoirs.

Changes at Barrett before and after 1998

The onset of trends in $AF_{[y]}$ and $SDD_{[w]}$ at Barrett was coincidental and abrupt (Fig. 7). A piecewise regression model with iterative search for the breakpoint (Crawley, 2007) in the $AF_{[y]}$ time series indicated that the breakpoint was in 1998 and that the slope of $AF_{[y]}$ over time changed from −1.1 d y^{-1} ($P < 0.01$; 1990–1998) to +9.6 d y^{-1} ($P < 0.001$; 1998–2011). After 1998, the annual pattern in anoxia at Barrett more closely resembled the more eutrophic Hodges (Fig. 8; online resource 12). Before 1998, the anoxic ratio at Barrett peaked during summer, reaching a maximum of 0.72. After 1998, the anoxic ratio peaked later, immediately after turnover, and regularly reached 1.0, indicating near-complete anoxia following the mixing of the anoxic hypolimnion with the epilimnion (Fig. 8). At Hodges, summer peaks in the anoxic ratio were similar in timing before and after 1998 and the anoxic ratio had already reached 1.0 twice before 1998 (1992 and 1997), though such events were more frequent after 1998.

Mean monthly anoxic ratio and *SDD* at Barrett changed significantly between periods of similar hydrodynamic conditions before 1998 (1993–1996) and after 1998 (2005–2011; Fig. 8; online resource 13). Pre-1998, *SDD* fluctuated between 1 and 7 m, and was greater than 3 m for more than a third of measurement dates (Fig. 8). In the post-1998 period, mean monthly *SDD* decreased in all months (online resource 13), as all but four measurements of *SDD* were less than 2 m (Fig. 8). Decreases in *SDD* at Barrett were largest between August and January, coinciding with both stable conditions in the late summer and with winter mixing. Anoxia increased and *SDD* decreased post-1998, despite a general reduction in stability.

Discussion

Effects of water depth and basin morphology on reservoir thermal dynamics

Water depth was the dominant control on thermal dynamics at all study reservoirs. Reservoirs fell on a single depth–stability regression line (Fig. 4) and correlations were highly significant between thermal and morphometric variables, but less significant with climatic variables (online resources 5–8). The only trends in thermal dynamics occurred at the reservoir (Morena) that experienced a monotonic reduction in volume and no concomitant trend in air temperature. The strong relationship between water depth and thermal regime in reservoirs with high WLF is

Table 5 Regression results for reservoir water quality characteristics as functions of fraction of watershed area burned (*F*), Schmidt stability (S), Secchi disk depth (*SDD*), duration of stratification (STR_{dur}), mean air temperature (T_A), epilimnetic temperature (T_E), year (YR), and hypolimnion mean depth ($\bar{Z}_H$) at Barrett (BA), Hodges (HO), Morena (MO), and Sutherland (SU)

Response variable	Reservoir	β: $STR_{dur[y]}$	β: $S_{[y]}$	β: $T_{A[y]}$	β: $\bar{Z}_{H[y]}$	β: $T_{E[y]}$	β: $SDD_{[w, y-1]}$	β: $YR_{[y]}$	LMG: $STR_{dur[y]}$	LMG: $S_{[y]}$	LMG: $T_{A[y]}$	LMG: $\bar{Z}_{H[y]}$	LMG: $T_{E[y]}$	LMG: $SDD_{[w, y-1]}$	LMG: $YR_{[y]}$	R^2	RMSE
Anoxic	BA	–	−0.19**	14.37*	21.48***	–	−23.33***	1.89**	–	0.07	0.06	0.17	–	0.27	0.27	0.85***	13.8
Factor	HO	–	–	–	–	11.58**	–	2.84***	–	–	–	–	0.13	–	0.55	0.68***	10.6
($AF_{[y]}$)	MO	0.35***	–	–	–	–	–	–	0.73	–	–	–	–	–	–	0.73***	17.6
	SU	–	–	10.82*	–	–	–	–	–	–	0.21	–	–	–	–	0.21*	13.5

Response variable	Reservoir	β: $S_{[w]}$	β: $F_{[y]}$	β: $STR_{[y]}$	β: $YR_{[y]}$	LMG: $S_{[w]}$	LMG: $F_{[y]}$	LMG: $STR_{[y]}$	LMG: $YR_{[y]}$	R^2	RMSE
Secchi disk depth ($SDD_{[w]}$)	BA	–	–	0.02*	−0.08**	–	–	0.15	0.24	0.39**	0.78
	HO	0.01*	–	–	–	0.26	–	–	–	0.26*	0.20
	MO	0.01***	–	–	–	0.58	–	–	–	0.58***	0.51
	SU	–	−0.01**	0.004***	–	–	0.20	0.41	–	0.61***	0.17

All variables are annual means; the subscript y indicates the mean was taken over a calendar year (Jan–Dec), the subscript "w, y − 1" indicates the mean was taken over winter months (Nov–Mar) in the months preceding and at the beginning of year y, and the subscript w indicates the mean was taken over winter months (Nov–Mar) at the end of year y and at the beginning of the next year (y + 1). The β is the regression parameter value and LMG is the relative contribution of each variable to the final R^2 (Grömping, 2006). Data for years when a reservoir did not stratify were excluded from the analysis

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

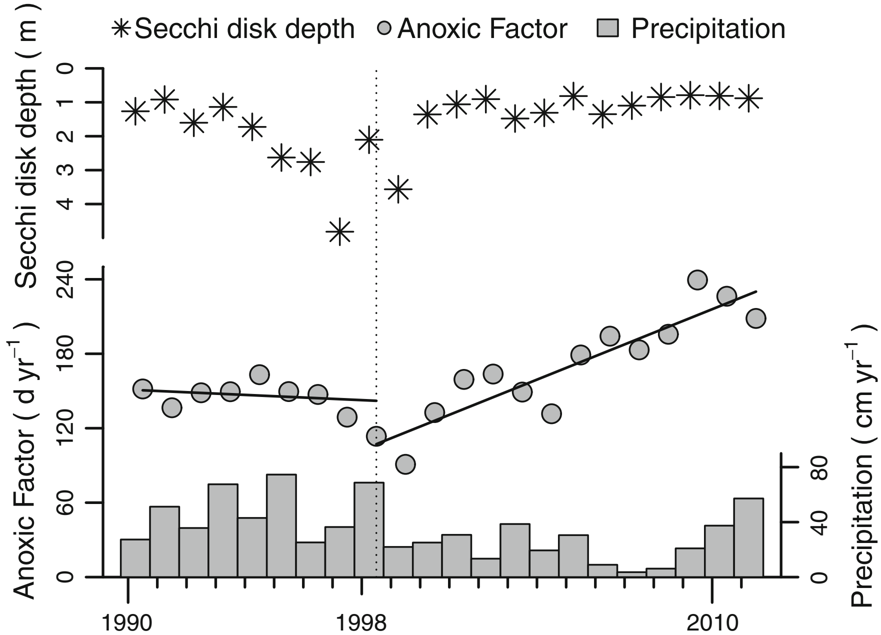

Fig. 7 Time series of Secchi disk depth ($SDD_{[w]}$), Anoxic Factor ($AF_{[y]}$), and precipitation at Barrett from 1990 to 2011. Values for $SDD_{[w]}$ are means for winter (Nov–Mar) and values for precipitation are sums by water year (Oct–Sep). Piecewise regression analysis indicated there is a breakpoint in the $AF_{[y]}$ time series in 1998 (*vertical dashed line*). The pre-1998 slope is -1.06 d y^{-1} ($P < 0.01$) and the post-1998 slope is 9.61 d y^{-1} ($P < 0.001$)

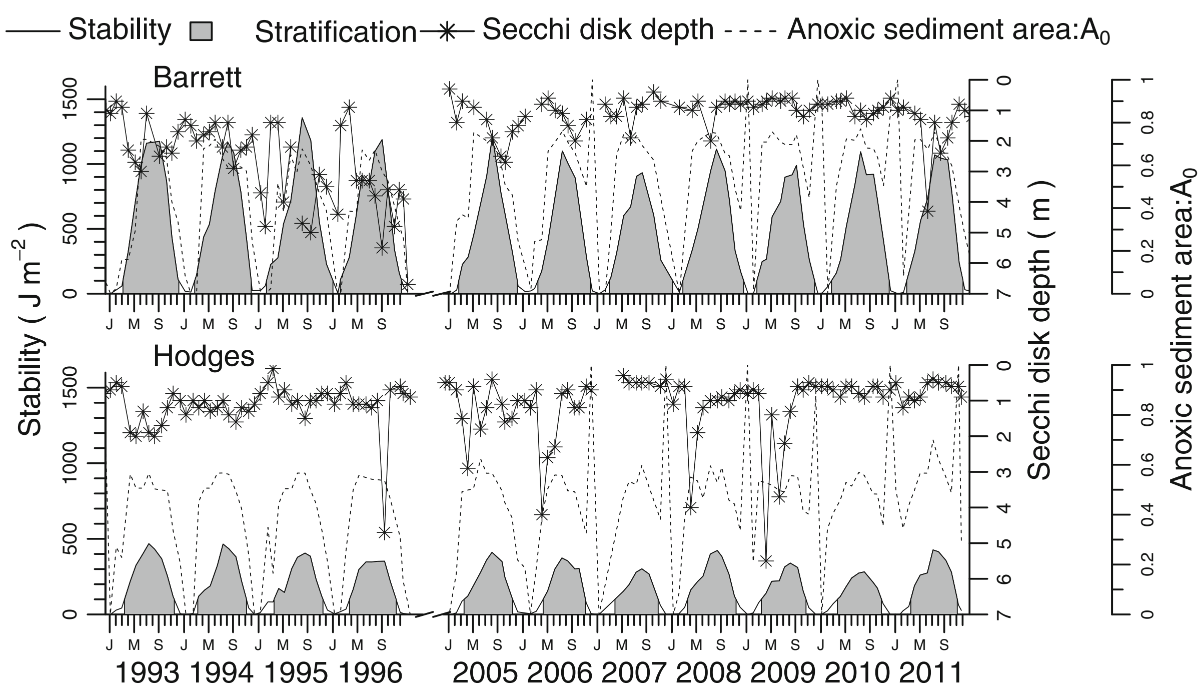

Fig. 8 Time series of Schmidt stability, Secchi disk depth (*SDD*), and anoxic ratio (anoxic sediment area:surface area) at Barrett and Hodges in two periods of similar stability, before and after 1998 (1993–1996 and 2005–2011, respectively). Piecewise regression analysis indicated that anoxia increased in severity and duration while *SDD* decreased at Barrett after 1998. Note the seasonal spikes in anoxia after turnover at Barrett in post-1998 period

consistent with other studies. Nowlin et al. (2004) found that in a managed reservoir, stability correlated better with reservoir volume than with air temperature, whereas Minns et al. (2011) found that in a natural bay, stability correlated better with air temperature than with volume.

Basin morphology modulated the impacts of water depth on thermal dynamics at all study reservoirs. The depth-stability relationship was stronger at the two deeper reservoirs (Barrett and Sutherland), leading to consistent development of stable, well-formed hypolimnia throughout the study period. As a result, at the two deeper reservoirs, $T_{H[y]}$ correlated significantly and positively with air temperature, which is typical of monomictic systems (Arhonditsis et al., 2004; Nowlin et al., 2004), and $T_{E[y]}$ correlated significantly and negatively with water depth. When water level decreases, epilimnetic volume decreases disproportionately more than surface area, and solar radiation received per unit area is distributed throughout a smaller depth, resulting in a warmer epilimnion (Rimmer et al., 2011). These relationships were not observed at the two shallower reservoirs (Hodges and Morena), where stratification occasionally failed to develop.

Air temperature, though statistically significant, was a weak and inconsistent predictor of stability at three of the four study reservoirs. Other studies, all of lakes rather than reservoirs, show positive correlations among air temperature, T_E, and thermal gradients in the water column (King et al., 1999; Snucins & Gunn, 2000), which is similar to observations at Hodges, where temperature was an important secondary predictor of stability after water depth. Decreased minimum air temperature has led to decreased stability and enhanced circulation of nutrients in a shallow prairie lake (Papst et al., 1980), and the same processes may have occurred to some extent at Hodges, though the trends in stability ($S_{[y]}$ and $S_{[w]}$) over time were not significant ($P > 0.05$).

Trends and controls on anoxia and transparency

Transparency at the study reservoirs was impacted by several processes. Transparency was lower in years when reservoirs did not stratify, presumably because lack of stratification allowed nutrients to circulate into the epilimnion. This suggests that reduced water depth, due to either increased withdrawal or reduced inflow during drought conditions, resulted in deterioration of water quality. Development in the watershed was highly correlated with lower transparency among watersheds, suggesting that development, both urban and agricultural expansion, led to deterioration of water quality. This finding is important, given the likelihood of future land cover change in the watersheds based on zoning plans for 2050 (online resource 4).

Different mechanisms likely underlied the progressive eutrophication at the two reservoirs that experienced increases in anoxia and decreases in transparency, given differences in the timing and seasonal signatures of anoxia and transparency, in basin morphology, and in land use in the watersheds. The increase in anoxia at the reservoir (Barrett) with the least developed watershed occurred rapidly and monotonically, starting in a single year, whereas the increase in anoxia at the reservoir (Hodges) with the most developed watershed was gradual over the study period. Below we explore the possible mechanisms behind the progressive eutrophication at the two reservoirs and compare the possible mechanisms with other literature.

Land use change and trophic status

Observed changes in land use likely had little impact on water quality at Barrett because increases in both low-density residential (from 0.9 to 2.0% of watershed area) and high-density residential area (1.6–1.7% of watershed area) over the study period were low and comparable to the increases observed at the two other reservoirs (Morena and Sutherland) that did not experience any change in anoxia or transparency. Commonly, a threshold of around 10% urbanization is exceeded before significant changes are observed in stream fauna (Riley et al., 2005). The small areal coverage of residential land use in Barrett watershed and the lack of change in anoxia at other reservoirs with similar land use change suggest that other mechanisms are responsible for the trends in $AF_{[y]}$ and $SDD_{[w]}$ at Barrett. Further investigation, including stormwater sampling above and below the new residential areas, is required to completely rule out an increase in allochthonous loading resulting from a small increase in urban area.

In Hodges watershed, development could have significantly increased allochthonous loading to the reservoir, given that development has previously been identified as a concern for water managers (Fox et al., 2002). Macrobenthic communities in streams throughout San Diego County were increasingly impaired along a low to high urbanization gradient (Viswanathan et al., 2010). Conditions were worse in winter than in fall, suggesting that urban runoff and stormwater runoff are important contributors to the degradation of water quality. A subsequent analysis by Voss et al. (2012) isolated chemical stressors (dissolved inorganic solids, such as nutrients and metals) as a significant explanatory variable for impaired biological integrity in the streams. Combined urban and rural residential development of Hodges watershed expanded from 17 to 23% of the watershed area from 1990 to 2009, though the few data points ($n = 2$ years) available for urban area in each watershed complicated hypothesis testing and caution must be used when interpreting causality. Urbanization largely replaced agricultural land and abatement of agricultural fertilizer use can significantly reduce nutrient export (Tong et al., 2009). However, we cannot rule out legacy sources of nutrients from agriculture, which can persist in groundwater for decades after agricultural land has been urbanized (French et al., 2006). Agriculture is a dominant control on stream water nitrate concentrations in San Diego County (Ta, 2012). Further research is required to document the relationship between land use, stream discharge, and stream water quality in the watershed.

Natural processes and trophic status

Natural watershed processes, including fire, precipitation, and runoff, can increase loading of sediment and nutrients to a reservoir, driving eutrophication over time. Fire and precipitation were significant controls on $SDD_{[w]}$ at Sutherland (Table 5); however, fire likely had little impact on water quality at the two watersheds with deteriorating water quality (Barrett and Hodges). Fires occurred between May and October at Barrett and Hodges, leaving the watersheds vulnerable to nutrient export during winter storms (Lane et al., 2008), though fire and precipitation were not significant in the $AF_{[y]}$ and $SDD_{[w]}$ regressions, there were no marked increases in frequency or areal extents of burns over the study period (online resource 14), and there was no significant increase in $AF_{[y]}$ or decrease in $SDD_{[w]}$ in wetter years (1990–2000) compared to drier years (2001–2011). This is consistent with other studies, where elevated nutrient concentrations in tributary streams after fire do not necessarily lead to elevated concentrations and eutrophication in receiving water bodies (Alexander, 2004; Feikema et al., 2011). Phosphorus can be adsorbed onto soil particles before reaching receiving waters, so nutrients mobilized after fire may be only redistributed within a terrestrial ecosystem, but not lost from it (Wright, 1976).

Low precipitation and low inflow may also increase risk of anoxia due in part to low rates of oxygenation by streamflow in dry years (Marcé et al., 2010). Although the onset of eutrophication at Barrett occurred during a period of lower precipitation (Fig. 7), the trend in anoxia was monotonic and did not correlate with precipitation over the study period. Reservoir age had no discernable impact on water quality at the study reservoirs, given that three of them were established in similar years (Barrett, 1922; Hodges, 1918; Morena, 1912), yet they experienced large variations in water quality. We conclude that natural processes had little or no effect on trends in eutrophication.

Trophic effects of fish introduction

Given the lack of significant changes in hydrodynamics, land use, or fire at the most pristine watershed (Barrett), we hypothesize that introduction of threadfin shad (*Dorosoma petenense*) in 1998, which coincided with the onset of trends in $AF_{[y]}$ and $SDD_{[w]}$, could have significantly increased algal production and contributed to anoxia. Shad are both planktivorous and detritivorous, as stomach contents suggest that shad engage in both pelagic and benthic feeding (Haskell, 1959; Gerdes & McConnell, 1963; Minckley, 1982). Changes in allochthonous loading were likely minimal because land use and burn extent in the watershed were both low and consistent over the study period. Increased release of nutrients from sediment and subsequent upward diffusion across the metalimnion were also not the most likely cause of increased algal production, particularly during summer. Nutrient release from sediment, represented by $AF_{[y]}$, was not significant in the $SDD_{[w]}$ regression and stability was high throughout the study period and also not significant in $SDD_{[w]}$ regression (Table 5).

Shad predation of zooplankton has led to increased chlorophyll concentrations and decreased *SDD* in other reservoirs in San Diego, including Hodges (White, 1991), where populations of threadfin shad became abundant quickly after introduction (Lafaunce et al., 1964; Dill & Cordone, 1997). There is a positive feedback among shad excretion, algal production, and shad reproduction. When total shad biomass is high, nutrient loading from excretion can exceed inputs from streamflow (Schaus et al., 2010) and, in other reservoirs, exceed the combined inputs from streamflow and sediment release (Nowlin et al., 2005). In three reservoirs in undeveloped watersheds, excretion of phosphorus by gizzard shad (*Dorosoma cepedianum*), the congener to threadfin shad, supported 18%, on average, of primary production (Vanni et al., 2006).

Other studies have documented that removing shad can reduce nutrient concentrations and algal production, increase transparency, and shift a reservoir toward oligotrophic conditions (Lepistö et al., 2006; Schaus et al., 2010). Piscovory by largemouth bass can reduce the population of shad, but there is little evidence suggesting that effects of piscovory cascade to the level of phytoplankton (Baca & Drenner, 1995). Although fish biomass can be a phosphorus sink, the ratio of phosphorus excreted to phosphorus sequestered in biomass in summer can remain high (Vanni et al., 2006). Further investigation is required to link grazing of zooplankton, translocation of phosphorus, and development of anoxia in the study reservoirs and to further substantiate management activity designed to reduce algal production and anoxia.

Conclusion

In this study, we used a long-term empirical data set to develop a conceptual model for understanding the dominant controls on reservoir thermal stability, anoxia, and transparency. Similar to other studies, we found that, in managed reservoirs, hydrodynamic regimes were controlled strongly by WLF and by basin morphology, and formation and temperature of hypolimnia were inherently different in deep compared to shallow basins under the same climate. In turn, in shallow reservoirs, stability was a significant control on algal production, as it minimized vertical transport of nutrients to the photic epilimnion. Our model accounts for the effects that processes in one season may have had on processes in another. At one reservoir, algal production in winter was a significant control on anoxia in summer, which in turn was a significant control on algal production in winter; at another reservoir, fires in autumn were a significant control on algal production in winter.

All study reservoirs were hypereutrophic and indicators of eutrophication increased significantly over time at two of them, after controlling for other relevant variables. Transparency correlated negatively with the fraction of developed watershed area, and the watershed with the most rapid urbanization showed progressive deterioration of water quality (increased anoxia). Contrary to our initial hypothesis, the reservoir with the most pristine watershed also showed progressive deterioration of water quality (both increased anoxia and decreased transparency). The introduction of fish coincided with the deterioration of water quality at the reservoir with the most pristine watershed, though further research is required to determine the mechanism and magnitude of the change due to fish zooplanktivory and phosphorus translocation. This study underscores the diversity of complex processes that can impact reservoir hydrodynamics and water quality in a Mediterranean climate, highlighting the direct roles played by reservoir management, above variability introduced by fluctuations in climate.

Acknowledgments We thank Jeff Pasek from the City of San Diego Water Department for providing the bulk of the data used in this study and for comments that helped with interpretation of the analyses. We also thank two anonymous reviewers for thoughtful comments. This study was supported by Agriculture and Food Research Initiative Competitive Grant No. 2011-38422-31204 from the United States Department of Agriculture National Institute of Food and Agriculture.

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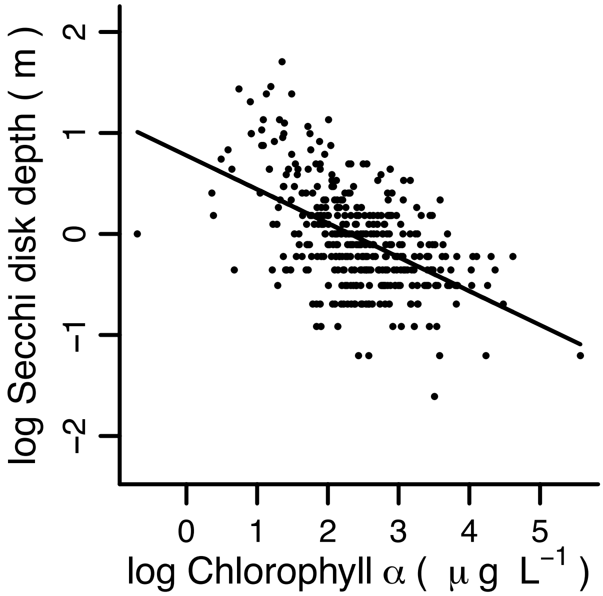
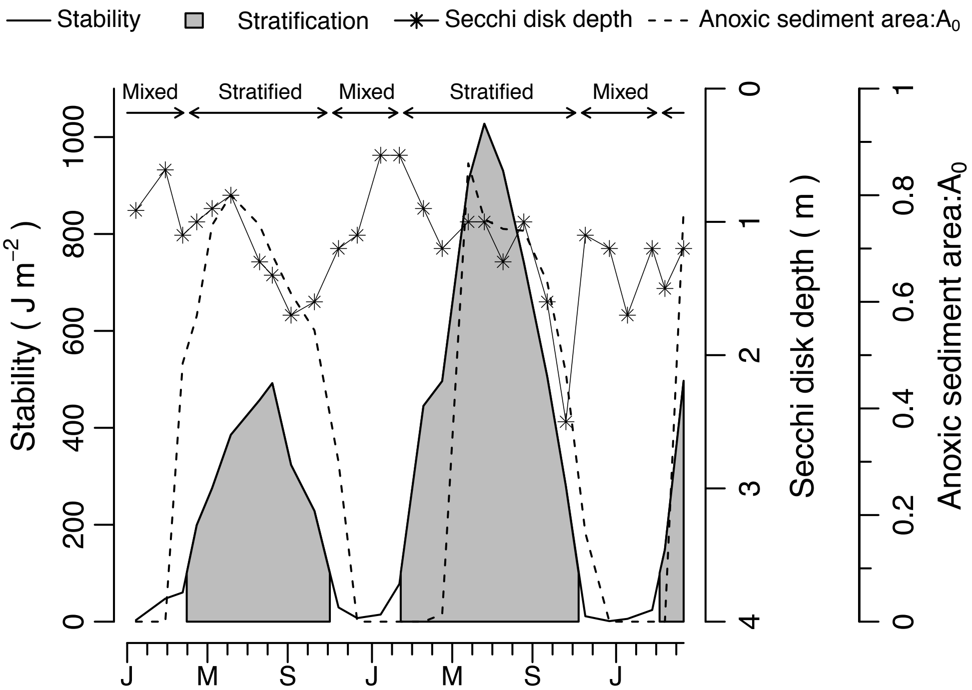
Online Resource 1. Physical characteristics of study reservoirs: volume (*V*); surface area (A_0)at capacity; maximum depth (Z_m); mean depth ($\bar{Z}$); and Osgood Index ($\bar{Z}/[A_0^{0.5}]$).

Reservoir	Location (lat, long)	Elevation (m asl)	V ($\times 10^6$ m^3)	A_0 (km^2)	Z_m (m)	$\bar{Z}$ (m)	$\bar{Z}/(A_0^{0.5})$ (m km^{-1})
Barrett	32.679254, −116.670492	482	48.0	3.5	41.9	13.8	7.4
Hodges	33.045264, −117.128410	98	51.2	6.0	29.1	8.5	3.5
Morena	32.685688, −116.547287	917	64.1	6.4	32.2	10.0	4.0
Sutherland	33.117856, −116.786642	629	36.6	2.3	40.6	16.3	10.9

Note: Values are maximum observed from 1990–2011.



Online Resource 2. Log-log relationship between chlorophyll α and Secchi disk depth. The equation (y = 0.77713 – 0.33563 × x) gives an Adj. R^2 = 0.27 (p < 0.001). The data shown are for all study reservoirs from 2002–2011.



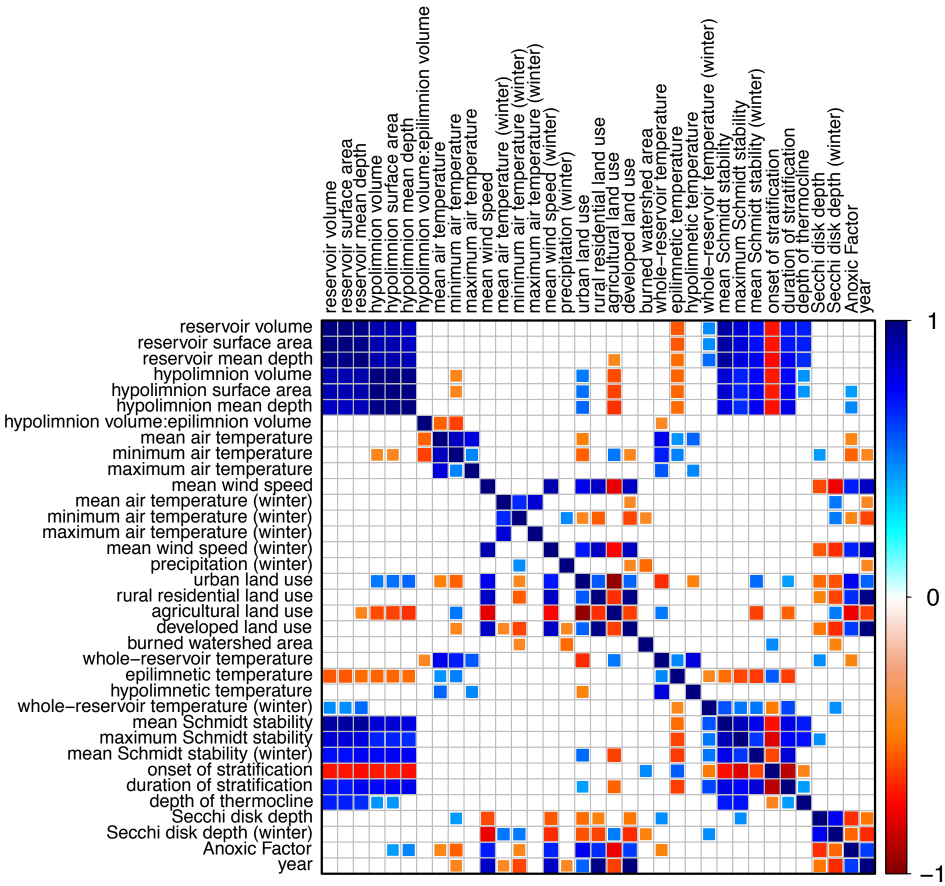
Online Resource 3. Typical seasonal cycles in Schmidt stability, Secchi disk depth (*SDD*), and anoxic ratio (anoxic sediment area:surface area) under variable reservoir storage conditions. Development of stability and anoxia follow a Jan–Dec cycle, whereas *SDD* increases during stratification (Mar–Nov) and decreases during mixed conditions (Nov–Mar). The data shown are for Sutherland Reservoir from Jan 1992–Apr 1994.

Online Resource4. Historical and projected land use, and historical areal extent of burns in study watersheds. Agricultural land use refers to extensive agriculture. Developed is the sum of urban, rural residential, agriculture, and managed parks.

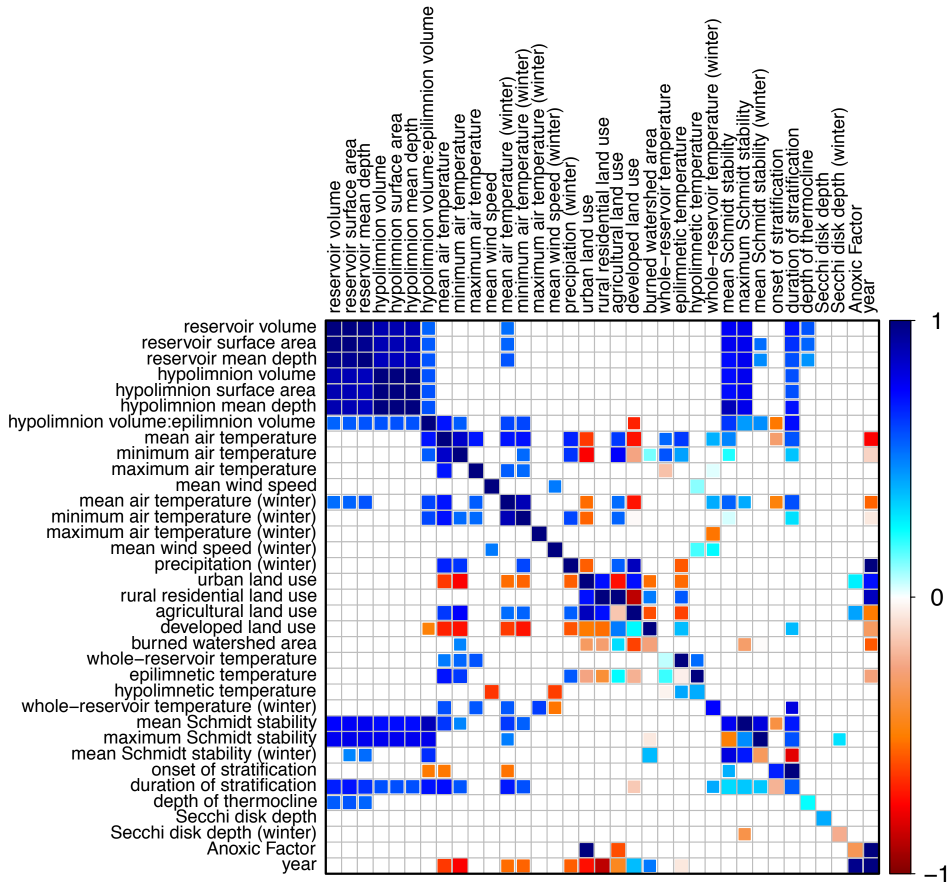
Watershed	Urban (%)			Rural residential (%)			Agriculture (%)			Developed (%)			Δ Developed (%)
	1990	2009	2050	1990	2009	2050	1990	2009	2050	1990	2009	2050	1990–2009
Barrett	1.6	1.7	1.8	0.9	2.0	6.8	1.1	1.1	0.7	3.6	4.8	9.3	1.2
Hodges	8.6	9.8	11.4	8.3	12.9	47.5	18.0	12.3	3.3	36.7	38.1	65.0	1.4
Morena	2.5	2.5	3.6	0.4	4.1	16.1	2.3	2.2	2.1	5.2	8.8	21.7	3.6
Sutherland	0.6	0.6	3.4	0.8	2.3	31.5	22.3	19.2	18.5	23.7	22.1	53.4	−1.6

Year	Watershed area burned (%)			
	Barrett	Hodges	Morena	Sutherland
1990	—	0.3	—	0.3
1991	—	0.0	—	0.1
1992	0.1	0.3	—	—
1993	—	13.3	—	—
1994	—	3.8	—	—
1995	—	—	—	—
1996	—	0.4	—	0.4
1997	0.1	0.6	—	—
1998	—	0.1	—	—
1999	0.1	0.1	—	—
2000	0.9	—	0.4	—
2001	—	—	—	—
2002	0.2	—	3.2	1.0
2003	10.1	17.1	—	8.7
2004	—	0.1	0.0	—
2005	0.4	0.0	—	1.7
2006	19.6	—	0.5	0.9
2007	5.5	66.0	1.8	42.5
2008	—	—	—	—
2009	—	—	—	—

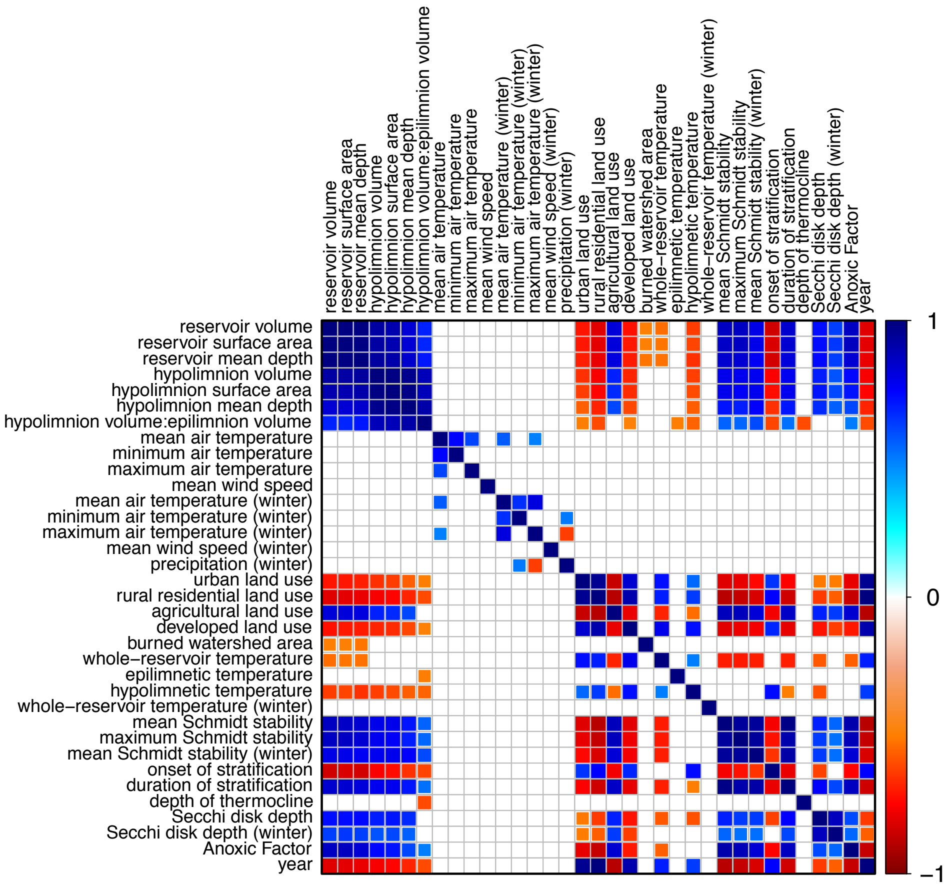
— indicates no fires reported that year.



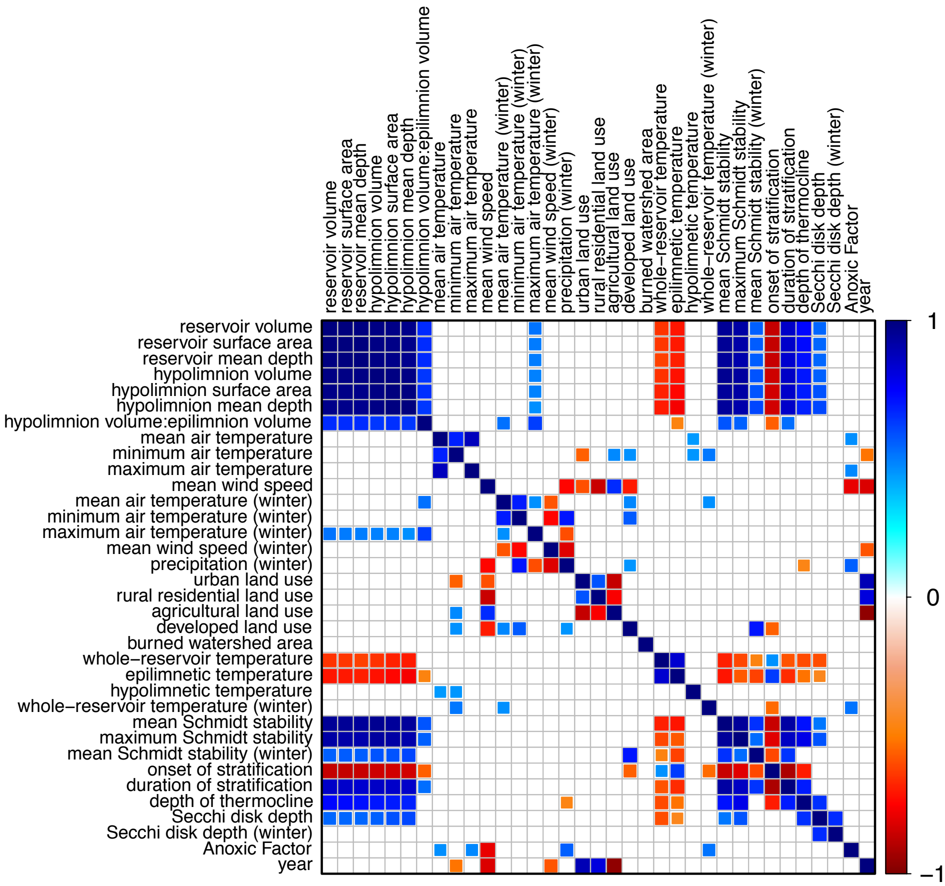
Online Resource 5. Spearman's ρ correlation matrix for Barrett. Variables are means aggregated by calendar year (Jan–Dec) or winter unstratified period (Nov–Mar). All listed coefficients are significant (α = 0.05). Agricultural land use refers to extensive agriculture.



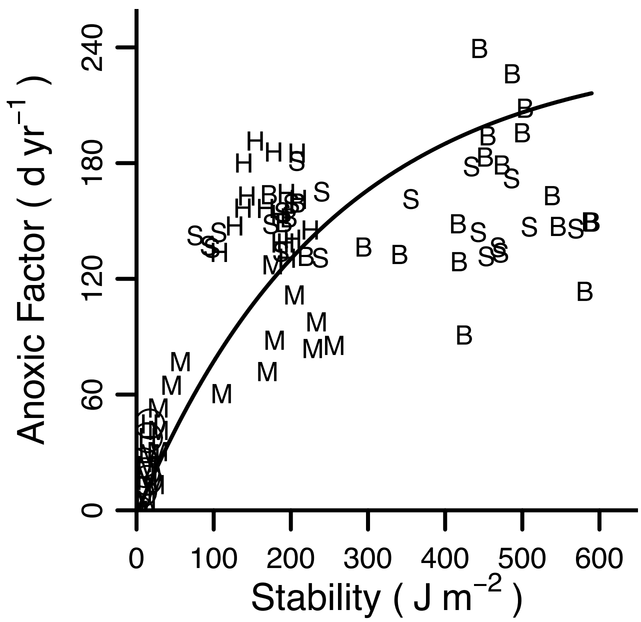
Online Resource 6. Spearman's ρ correlation matrix for Hodges. Variables are means aggregated by calendar year (Jan–Dec) or winter unstratified period (Nov–Mar). All listed coefficients are significant (α = 0.05). Agricultural land use refers to extensive agriculture. Data for years when the reservoir did not stratify were excluded from the matrix.



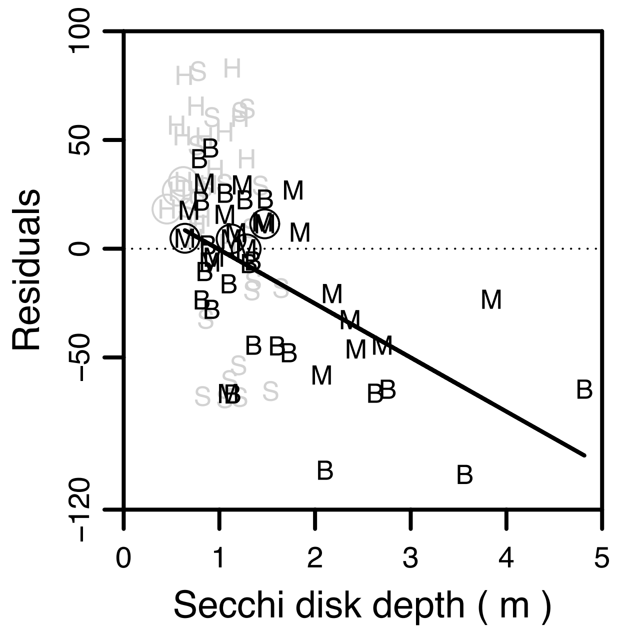
Online Resource 7. Spearman's ρ correlation matrix for Morena. Variables are means aggregated by calendar year (Jan–Dec) or winter unstratified period (Sep–Mar). All listed coefficients are significant (α = 0.05). Agricultural land use refers to extensive agriculture. Data for years when the reservoir did not stratify were excluded from the matrix.



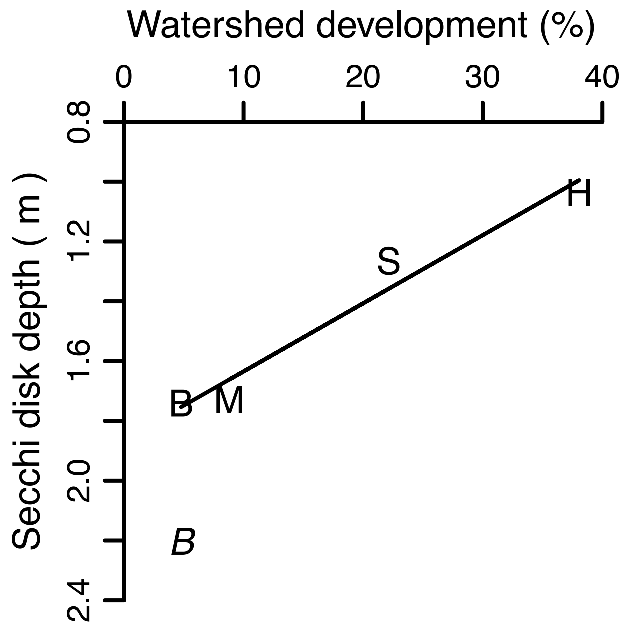
Online Resource 8. Spearman's ρ correlation matrix for Sutherland. Variables are means aggregated by calendar year (Jan–Dec) or winter unstratified period (Nov–Mar). All listed coefficients are significant (α = 0.05). Agricultural land use refers to extensive agriculture.



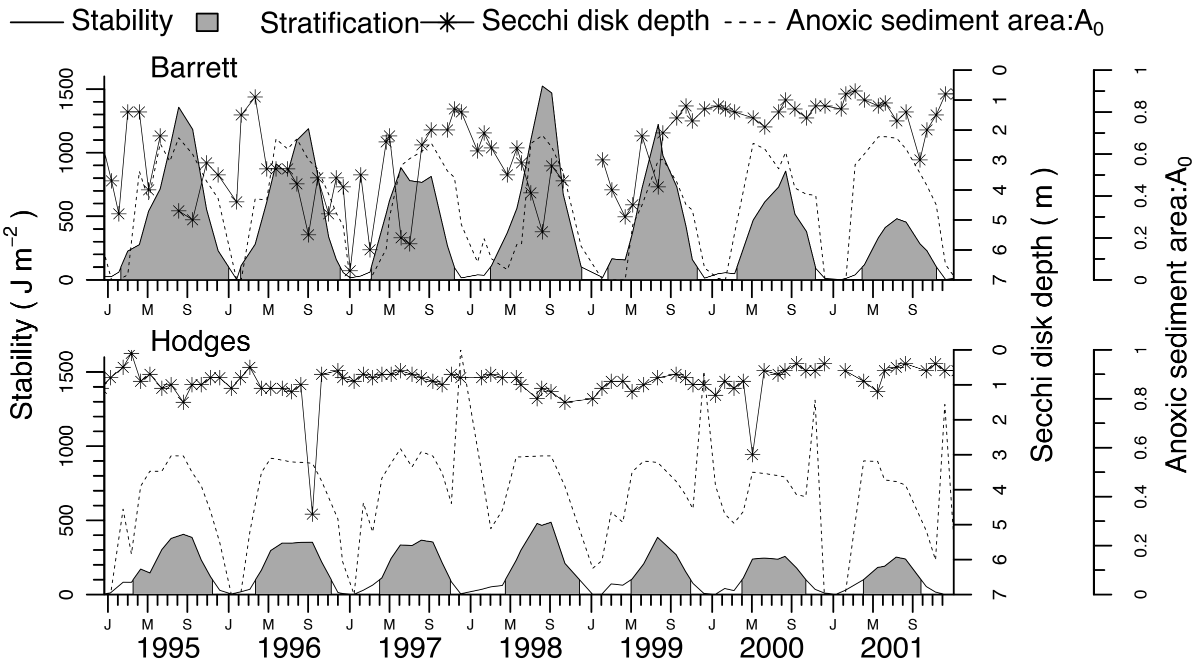
Online Resource 9. Relationship between mean annual (Jan–Dec) Schmidt stability and annual Anoxic Factor (AF) with non-linear regression model, given by the equation, $y = 239\left(1 - e^{-0.004(x - 1.954)}\right)$, where e is the base of the natural logarithm. The lower limit of x is 1.954, the minimum observed mean annual stability (J m^{-2}), and the upper limit of y is 239, the maximum observed AF (d yr^{-1}). Points in circles indicate years when a reservoir did not stratify.



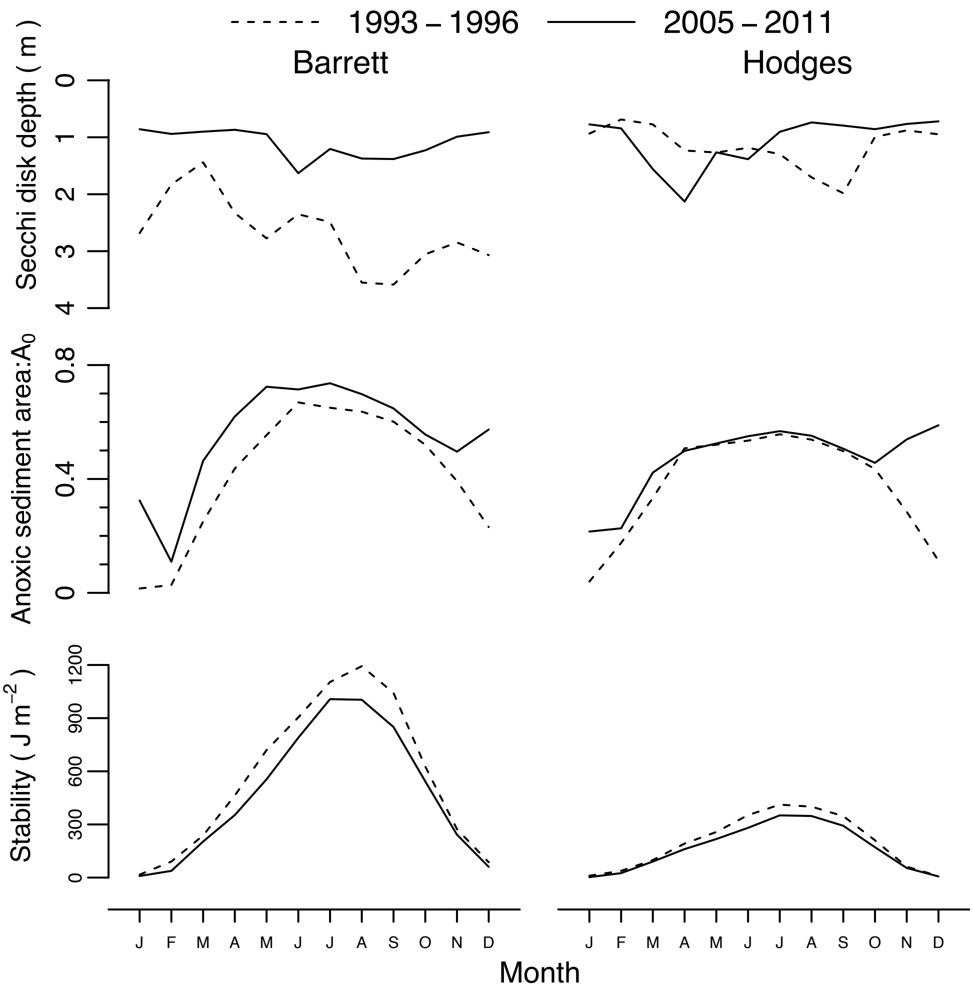
Online Resource 10. Relationship between winter (Nov–Mar) Secchi disk depth and residuals of the regression of Anoxic Factor on mean annual (Jan–Dec) Schmidt stability. The relationship was significant for Barrett and Morena, both for which a combined regression yielded an equation (y = 24.37 – 24.812 × x) that gives an Adj. R^2 = 0.34 (p < 0.001). Hodges and Sutherland are shown in grey. Points in circles indicate when a reservoir did not stratify.



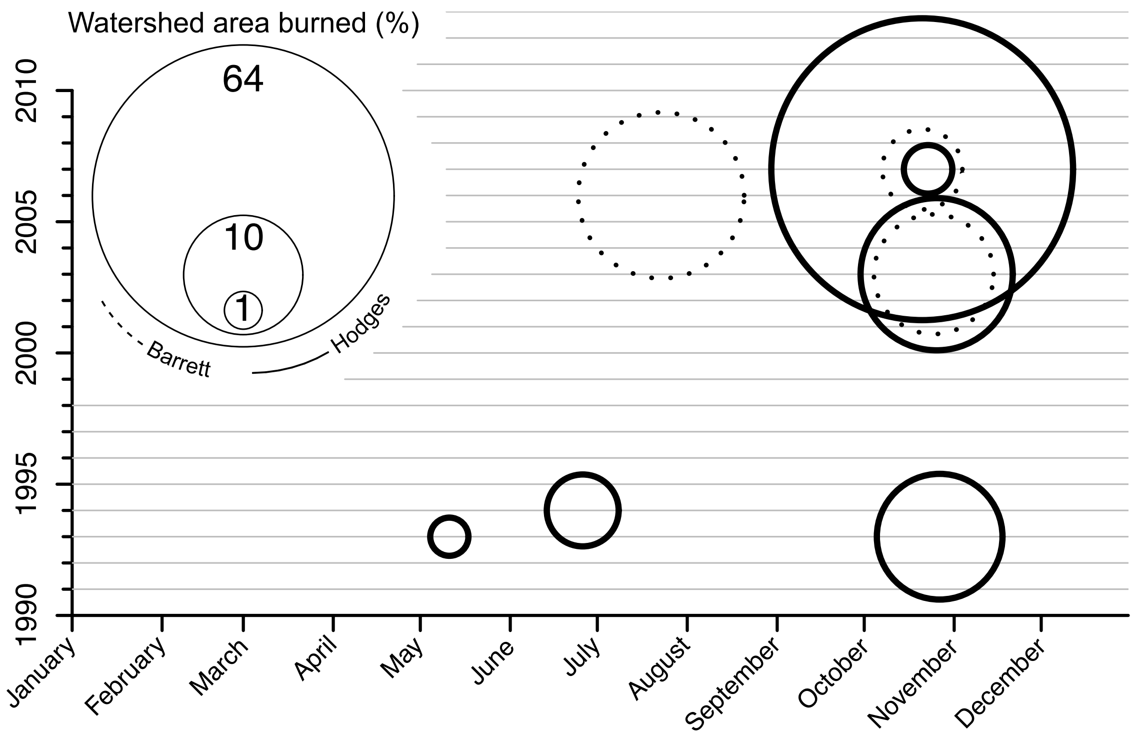
Online Resource 11. Relationship between areal percentage of total development in a watershed (in 2009) and mean Secchi disk depth (*SDD*) over the study period. The equation (y = 1.862608 – 0.022791 × x) gives an Adj. $R^2 = 0.94$ ($p < 0.05$). The italicized "B" indicates the mean *SDD*, pre-1998. Data for years when a reservoir did not stratify were excluded from the analysis.



Online Resource 12. Time series of Schmidt stability, Secchi disk depth (*SDD*), and anoxic ratio (anoxic sediment area:surface area) at Barrett and Hodges from 1995–2001. Piecewise linear regression analysis indicated that anoxia increased in severity and duration while *SDD* decreased at Barrett after 1998.



Online Resource 13. Monthly average Secchi disk depth (*SDD*), anoxic ratio (anoxic sediment area:surface area), and Schmidt stability at Barrett and Hodges in two periods of similar stability, before and after 1998 (1993–1996 and 2005–2011, respectively). Piecewise linear regression analysis indicated that anoxia increased in severity and duration while *SDD* decreased at Barrett after 1998.



Online Resource 14. Temporal distribution of fires in Barrett and Hodges watersheds from 1990–2010. Fires that burned less than 1% of their respective watershed area are not shown.