Changes across a Decade in Size, Growth, and Body Condition of Western Pond Turtle (*Actinemys marmorata*) Populations on Free-flowing and Regulated Forks of the Trinity River in Northwest California

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Water diversions can disrupt flows and alter thermal regimes changing seasonal patterns that signal the onset of life-history functions of native organisms and compromise the fitness of their populations. We compared size, growth, relative mass, volumetric body condition, and reproductive status of Western Pond Turtles (*Actinemys marmorata*) across a decade on two forks of California's Trinity River, one regulated and the other free-flowing. Turtles on the regulated fork experienced flows designed to accommodate anthropocentric demands, whereas those on the free-flowing fork experienced natural hydrologic cycles and seasonal warming. July water temperatures averaged 8.6°C colder on the regulated fork due to hypolimnetic releases. Turtles on the colder regulated fork grew more slowly and were smaller at similar ages compared with those on the free-flowing fork, a pattern that was exacerbated across the decade. Female relative mass (RM) across the decade did not differ between forks, whereas male RM was greater on the free-flowing fork only in the 1990s. In the 2000s volumetric body condition of females on the regulated fork differed significantly from males on both forks and females on the free-flowing fork. Females on the regulated fork appeared to be assimilating more resources possibly in response to colder water. Fewer females on the regulated fork were gravid and, due to smaller size, likely carried fewer eggs. The percent of gravid females on both forks declined significantly across the decade. We found additional evidence of a wider regional effect with differences in RM shifting from positive to negative for both sexes on both forks. We did not collect evidence that would explain these phenomena but these changes strongly suggest that trophic relationships of the turtles in the greater region are being adversely influenced.

V ARIATION in body size, growth rate, and reproductive status can indicate important differences in the fulfilment of life-history functions among populations (Stearns, 1992), differences that can have profound implications for Darwinian fitness (Stearns and Koella, 1986). Extrinsic factors that affect body size can influence individual fitness and ultimately have a negative effect on long-term population viability. Larger body size can infer advantages such as ability to consume larger prey items, dominance in competitive interactions (Bury and Wolfheim, 1973; Cadi and Joly, 2003), increased reproductive output (Gibbons et al., 1981; Iverson, 1992), and maintenance of thermal inertia during environmental extremes (Stevenson, 1985; Polo-Cavia et al., 2009). Because turtles have a rigid shell, larger body size can infer specific selective advantages. In particular, a larger carapace can exceed gape limits of many predators (e.g., mink, otter, raccoon, fox; all present in our study area; Swingland and Coe, 1979; Holland, 1994), and allow females to carry more or larger eggs (Congdon and Gibbons, 1983, 1985; Iverson, 1992; Iverson et al., 1997).

The Western Pond Turtle (*Actinemys = Emys* [formerly *Clemmys*] *marmorata*) was once widespread across the Pacific slope of North America, occurring in a wide variety of wetlands wherever aquatic habitats were available for at least part of the year, and where terrestrial areas for nesting, over-wintering, and aestivation were close and accessible. Currently, with some exceptions where new habitat and new populations of turtles have arisen through the building of artificial water catchments, populations of *A. marmorata* are in decline in much of their historic range due to habitat conversions, water diversions, agricultural development, urbanization, and competition from non-native species (Jennings and Hayes, 1994; Bury and Germano, 2008; Bury et al., 2012). Many rivers and streams in the central portion of the range of the species in northern California still provide strongholds of pond turtle populations. However, even in lightly impacted areas, persistence can be threatened by dams and water diversions that change natural flow cycles (Poff and Zimmerman, 2010) and aquatic thermal regimes (Olden and Naiman, 2010). Large dams can result in significant alterations to aquatic habitats, both at the impoundment site and in downstream environments (Magilligan and Nislow, 2005; Ashton, 2008; Poff and Zimmerman, 2010).

The Main Fork of the Trinity River in northern California was dammed in 1963 to divert water for agriculture and electric power generation, resulting in numerous hydro- and geomorphologic changes to the system below the dam including increased channelization, lower water temperatures, lower discharge, reduced flood magnitudes, and blocking salmonid migration (Hampton, 1995; Trush et al., 2000). Attenuation of the annual pre-dam natural flood cycle necessary to maintain a dynamic alluvial system has allowed streamside encroachment of woody riparian vegetation; this has led to stable berm development and channelization of the river, with subsequent reductions of shallow edge water and back channel environments (Evans, 1980), to the detriment of native fishes and riparian wildlife (Lind et al., 1996; Reese and Welsh, 1998a; McBain and Trush, 2000). To promote an anadromous fishery below the dam, cold water is released from near the bottom of the reservoir (i.e., hypolimnetic releases) resulting in unnaturally cold water temperatures in the river channel

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during the summer; these temperatures differ greatly from those of the warmer pre-dam conditions, a difference that increased following the Record of Decision (USDI, 2000), which increased the water allocation for hypolimnetic releases along with ongoing channel rehabilitation to benefit native fish and wildlife (McBain and Trush, 2000). Alterations to the thermal regime due to deviations from the natural hydrologic cycle have disrupted the life cycles of many riverine organisms (e.g., Lind et al., 1996; Fuller et al., 2011; Hunt et al., 2013; Wheeler et al., 2014) including pond turtles. However, because Western Pond Turtles are long-lived organisms, negative impacts to their populations can take decades to become evident (Rowe, 2008; Tuberville et al., 2014).

Three decades after dam construction, a demography study found evidence of reduced recruitment of young turtles into the Main Fork population compared with the population on the free-flowing South Fork (Reese and Welsh, 1998a). We re-sampled the same two populations to re-assess earlier findings on life-history parameters, and to seek evidence of differences between the populations in these parameters that were previously undetected or that may have occurred over the subsequent decade. Changes in turtle demography since Reese and Welsh (1998a) will be the subject of a future paper. In this study we examined how alterations of the flow regime have affected size, growth rate, condition indices, and reproductive status of turtles on the regulated Main Fork of the Trinity River by comparing these attributes with those on the un-regulated South Fork.

Carapace length provides a relative index of turtle body size, and it is not prone to the seasonal fluctuations that occur with body mass of temperate freshwater turtles. Maximum straight-line carapace length is commonly used to compare body size of turtles among systems (Lubcke and Wilson, 2007; Germano and Bury, 2009; Bury et al., 2012). Western Pond Turtle populations have shown variability in body size in different environments (Lubcke and Wilson, 2007; Germano and Bury, 2009; Bondi and Marks, 2013). In an initial re-visit of turtle populations on the Trinity River a decade after Reese and Welsh (1998a), we noted smaller carapace lengths in turtles on the Main Fork compared with the South Fork; this suggested possible impacts to fitness not detected in the earlier study. Consequently, we initiated this three-year study to compare metrics of turtle status across the decade and between the two forks to determine if, and where, there have been significant changes over the intervening time. Comparing size, growth, relative mass, volumetric body condition, and reproductive status of marked, known-age turtles across the two study periods and two forks allowed us to test the hypothesis that changes in these life-history parameters have occurred over the past decade to the population on the regulated fork but not the population on the unregulated fork. By using the same sampling protocols and study reaches as the earlier research, we compared differences in life-history parameters of turtles captured in this current effort with those reported by Reese and Welsh (1998a) and added several new metrics.

MATERIALS AND METHODS

Study region.—Prior to damming in 1963, the Main Fork (MF) of the Trinity River (Fig. 1) experienced dramatic impacts initially from large-scale placer mining, followed by hydraulic and later dredge mining. The South Fork (SF) remains free-flowing, although this watershed has an
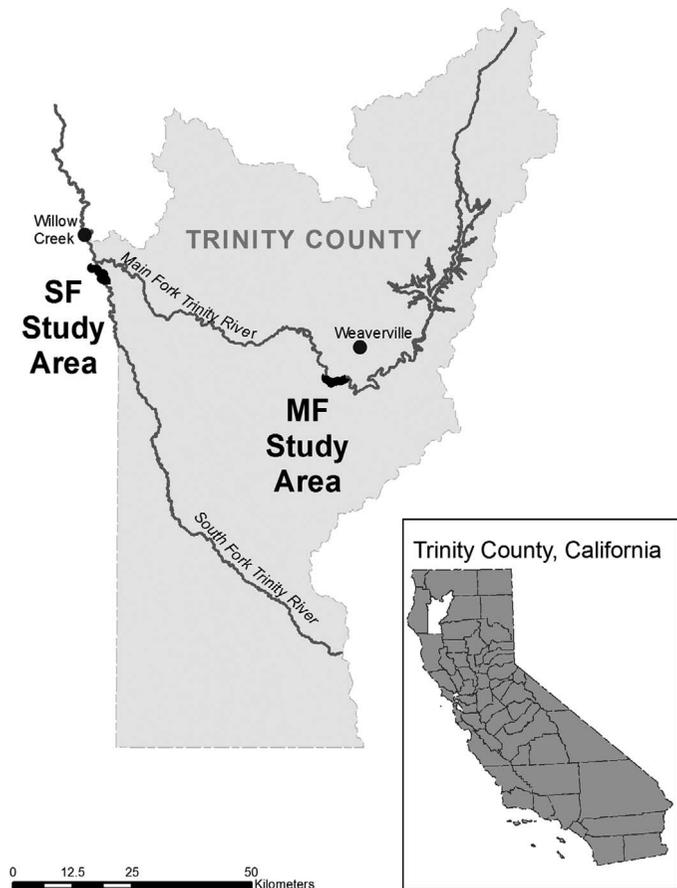
Fig. 1. Study reaches on the Trinity River, Trinity County, California. The regulated Main Fork (MF) study reach runs from 38.2 km to 43.8 km below the lower dam. The unregulated South Fork (SF) reach runs from 9.0 km to 0. 4 km above the confluence with the Main Fork.

extensive history of timber harvesting, ranching, and natural disturbances, such as landslides and fires (Welsh et al., 2010). These two major river forks have comparable drainage areas and prior to the dam, had similar average annual flows (2460 km² and 2968 km² [1.1 million and 1.2 million acre-feet], respectively [Reese and Welsh, 1998a]). Both forks flow through mixed hardwood-conifer forests consisting of oak (*Quercus* spp.), madrone (*Arbutus menziesii*), Douglas-fir (*Pseudotsuga menziesii*), gray pine (*Pinus sabiniana*), and ponderosa pine (*Pinus ponderosa*). The regulated Main Fork has dense shoreline vegetation, with large woody debris providing most of the available turtle basking substrates, whereas the free-flowing South Fork is bedrock-dominated with sparse shoreline vegetation and emergent rocks provide most turtle basking sites (Reese and Welsh, 1998b). Characteristics of the riparian areas differ between the two forks, in part due to geology, but primarily as a result of the dam. While both forks experience winter rain and spring snow-melt peak flows, the Main Fork is relatively more snow-melt driven because it drains the higher elevation Trinity Alps.

Documenting thermal regimes.—We placed data recording thermistors (HOBO, Onset Computer Corporation) at the up and downstream ends of the study reaches of both forks to record water and air temperature at 1 or 2 hr intervals for each sampling season during the summers of 2005, 2006, and 2007. We used mean maximum water temperatures

from July, averaged across the three years, to compare thermal regimes between the two forks.

Field techniques.—We conducted capture-mark-recapture surveys of pond turtles during the summers of 2005, 2006, and 2007. Our sampling methods and locations were based on protocols from 1991–1994 (Reese and Welsh, 1998a, 1998b) when many of these turtles were initially marked. Efforts were taken to replicate the earlier field methods, and one of the current authors (DTA) participated in the field phase of both studies. We conducted four surveys on each fork in 2005, five in 2006, and four in 2007. Each survey typically took three consecutive days on each fork, alternating weekly between forks during June, July, and August. The sampling occurred between 1000 and 1800 hr, except in mid-summer when lighting conditions permitted effective sampling to 2000 hr in some locations. We used kayaks to access study reaches. Two people, one along each river bank, used a mask, snorkel, and fins to swim and capture turtles. Divers worked along each bank to 4 m out into the river channel, searching under boulders, logs, undercut banks, and root wads, and watching for basking turtles. Turtles were hand-captured and passed to a third person in a kayak to process and release at the capture site.

Documenting capture events.—We recorded time, location, position, and behavior (e.g., under a boulder, log/wood, in the open, basking) for each capture. We measured mass and shell morphometrics (Appendix 1) and described and photographed injuries or health abnormalities. For most captures, we took digital photographs of carapace, plastron, and a close-up of the posterior half of the plastron using a 15 cm ruler for scale. Photographs were linked to individual records in a database and were useful for confirming individual identity and verifying annuli counts used to determine specific ages. We determined sexes by the presence of sexually dimorphic characteristics, which develop in turtles as they mature (Bury et al., 2012). We used inguinal palpation on adult females (>125 mm carapace length [CL]) captured in June or July to determine reproductive condition; this allowed us to calculate the proportion of mature females that were gravid and compare reproductive status of populations on each fork and across the decade. Because of the lack of sexually dimorphic characteristics in young individuals, external examination was not reliable and we recorded sex as unknown. In this region, pond turtles are thought to mature between six and ten years old (Holland, 1994). However, the exact age at maturation is not known, and size and/or age of maturation likely differ for the sexes and may also differ between the two forks.

Annuli counts and marking.—Temperate freshwater turtles commonly exhibit a pattern of rapid growth in the warm season followed by a lag during the cold season, producing annual rings (annuli) on individual scutes and shields that comprise the carapace and plastron (e.g., Sexton, 1959; Gibbons, 1967; Germano and Bury, 1998). We determined age of individual turtles by counting annuli (Gibbons, 1990; Reese and Welsh, 1998a; Stone and Babb, 2005). While this method is not perfect (Litzgus and Brooks, 1998; Wilson et al., 2003), it has been shown to provide an accurate index of age for younger Western Pond Turtles, up to ten years of age or more, depending on local environmental conditions

that can influence growth rates and annuli wear (Bury and Germano, 1998). Annuli do not provide a reliable age for older turtles because as growth slows, annuli narrow and are often difficult to accurately discern, and over time wear can erase the ridges of earlier annuli (Germano and Bury, 1998). Turtles on the South Fork use rocky substrates for basking, whereas those on the Main Fork used primarily wood (Reese and Welsh, 1998b). This resulted in more wear on the plastron of South Fork turtles which is evident by about eight years of age, while on the Main Fork annuli were readily discernible well into the teens. Consequently, we could not confidently count annuli on turtles > 8 yr old on the South Fork. When wear on annuli precluded accurate counts, we did not use those animals in analyses based on age. We marked individual turtles following methods of Cagle (1939), using a revised numbering scheme developed by Holland (1994).

Analyses.—To assess differences in size and growth of turtles from the free-flowing South Fork and those from the regulated Main Fork, we compared mean carapace length by fork and decade using fixed effects GLM ANOVA on three subsets of a combined 1990s and 2000s dataset: 1) adult males and females > 125 mm CL using data from the first capture only to compare with previous research (Reese and Welsh, 1998a; Germano and Bury, 2009); 2) largest adult males and females (top 10% or upper decile) using the last capture to compare maximum sizes; and 3) young turtles 2–8 yr of age regardless of sex to compare the size-at-age of turtles where we could most confidently determine age with annuli counts using the last capture in each year. Size dimorphism between the sexes is known in this species (Lubcke and Wilson, 2007; Germano and Bury, 2009), but typical dimorphism could be over-ridden by response to disturbance (including changes in the thermal regime), so we included sex as a factor in size analyses of adults (i.e., those > 125 mm CL and the upper decile).

The first analysis employed a size cut-off of 125 mm CL to define adults (following Reese and Welsh, 1998a); we excluded 28 turtles > eight years or > 125 mm CL with unknown sex resulting in a sample size of 489 turtles. Given our conjecture that differences in thermal regimes on the two forks may be differentially influencing the growth of individuals, using the same size cut-off to define adults on both forks could preclude a valid test of this hypothesis with our first analysis if the differences were slight. Therefore our second and third analyses focused on the extremes of the turtles we captured: those well beyond the maturation period (i.e., the upper decile based on CL) and those prior to expected maturation (i.e., 2–8 yr olds based on annuli counts). By comparing the largest turtles of each sex from each fork and decade, we eliminated potential bias due to errors in sex identification that may have occurred with smaller turtles that were not fully dimorphic. This allowed us to compare adults of maximum size ($n = 56$) relative to three factors (fork, decade, sex), and make a direct comparison with similar research on the same species in other regions (Bury et al., 2010). To compare and analyze size at a given age during early growth years, and the period of most recent river management on the Main Fork, we used field annuli counts and recapture history to determine ages of 326 turtles captured at 2–8 yr of age. For turtles captured in the 2000s, we also used digital photographs of the plastron to confirm field annuli counts. To test for

differences in size of young turtles between forks and across the decade, we used analysis of covariance (ANCOVA), with CL as the dependent variable, fork and decade as fixed predictor variables, and age (2–8 yr) as a covariate.

Adult body size may be constrained by juvenile growth rates in the early years (Gibbons, 1967), so we conducted growth analysis on young turtles of known age. We assessed differences in growth rate for 2–8 yr old turtles (the same group as the previous analysis of size). The young of this species follow a linear growth pattern; consequently, we applied a linear growth model to these turtles (see Lester et al., 2004; Shuter et al., 2005; Quince et al., 2008a, 2008b). We compared mean CL for each age 2–8 yr, to test differences between the forks and decade. We used these means to produce pre-maturation growth rates for each fork by decade.

Body condition indices are proxies for fitness (Peig and Green, 2010; Rohr and Palmer, 2013). We used body condition indices to approximate body mass associated with energy reserves after correcting for body size of adult turtles. To account for potential scaling issues associated with ontogeny (see Peig and Green, 2010), we limited our body condition analysis to full size adults (>125 mm CL). To reduce the influence of gravid females and turtles still replenishing resources lost during over-wintering (see Kozlowski et al., 2004), we did not use data from captures prior to 1 July. If an individual was captured more than once in a year, we used only the last capture. Due to sexually dimorphic differences in shell shape in adults (Bury et al., 2012), we calculated residuals separately for females and males. We used the residuals of ordinary least squares linear regression of log-transformed mass (LogWT) against log-transformed carapace length (LogCL) as a body condition index (Schulte-Hostedde et al., 2005; Băncilă et al., 2010). We hereafter refer to this metric as relative mass (RM) to distinguish it from the volumetric body condition described below. For each sex, we compared RM between forks and across the decade using fixed effects GLM ANOVA.

In the 2000s we added the variables shell height (SH) and carapace width (CW) to the morphometric measurements we collected, allowing for a more refined analysis of body condition using a volumetric formula to compare values between forks. We calculated volumetric body condition index (vBCI) as follows:

$$vBCI = Weight/(\pi * (CL) * (SH) * (CW)/6000)$$

with length in millimeters and weight in grams (Loehr et al., 2007). Compared to a RM based on the ratio of weight to length, this volumetric index provides a ratio that better approximates the body density of chelonians (Loehr et al., 2007). However, because the volumetric measurements do not fully account for sex differences in shell shape (e.g., convex plastron, roundness of dome), we analyzed the sexes separately. Again, we limited our analysis to captures post-June to focus on turtles that had likely already replenished over-wintering reserves. We compared the forks for each sex using fixed effects GLM ANOVA.

We used 607 palpation events recorded in June and July to evaluate the reproductive frequency for populations on the two forks and across the decade. Because small turtles are difficult to palpate, we used only females > 125 mm CL. Groups were tested for differences in proportion of gravid females using fixed effects GLM ANOVA.
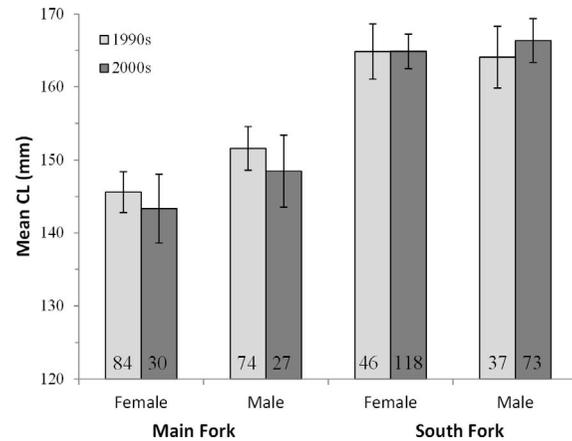
Fig. 2. Mean carapace length (CL) for adults of known sex > 125 mm by fork and decade (males: $n = 211$; females: $n = 278$). Error bars are 95% confidence intervals. Numbers on bars are sample sizes.

We used Excel and Access (Microsoft, 2007) to calculate residuals and produce graphs. All other analyses were conducted in NCSS 2000 (Hintze, 2004). Alpha was set at 0.05 for all tests. We used Fisher's LSD multiple comparisons test for all multiple comparisons. Effect sizes were calculated as ±1.96 * SE (i.e., 95% confidesnce interval [Nakagawa and Cuthill, 2007]) and reported as error bars on histograms.

RESULTS

Thermal regimes.—July maximum water temperatures on the regulated Main Fork averaged 17.3°C from 2005–2007, while on the unregulated South Fork maximum temperatures averaged 25.8°C during this same period, an average difference of 8.6°C.

Size and growth comparisons.—General trends we found in mean carapace lengths (CL) over the course of this study were: (1) males were consistently larger than females; (2) turtles on the South Fork were larger than those on the Main Fork; and (3) the size of Main Fork turtles declined across the decade, whereas those on the South Fork did not (Table 1). Adult males had significantly greater CLs than adult females ($F_{1,488} = 4.90$, $P = 0.027$), with the difference between sexes more extreme on the Main Fork where males had 3.6% greater CLs than females, but only 0.9% greater than females on the South Fork (fork x sex, $F_{1,488} = 3.78$, $P = 0.052$; Fig. 2). Adult turtles > 125 mm CL on the unregulated South Fork had significantly greater CLs than on the regulated Main Fork ($F_{1,488} = 176.60$, $P < 0.0001$; Fig. 2). Although differences across the decade for these turtles were not statistically significant ($F_{1,488} = 0.33$, $P = 0.567$), females on the South Fork had an average of 13% greater CLs than females on the Main Fork in 1990s, with this difference increasing to 15% in the 2000s. The difference in length for males also increased across the decade from 8% greater CLs on the South Fork in the 1990s to 12% greater in the 2000s.

For the largest 10% of turtles (i.e., upper decile; Table 1), the sexes were significantly different ($F_{1,55} = 32.11$, $P < 0.0001$), and the South Fork turtles had significantly greater CLs than the Main Fork turtles ($F_{1,55} = 734.27$, $P < 0.0001$). The upper decile size of South Fork males averaged 10.8% greater than Main Fork males in the 1990s and 15.7% greater in the 2000s; females were 13.1% greater

Table 1. Means, standard errors (SE), and sample sizes (*n*) of life-history attributes of Western Pond Turtles (*Actinemys* [*Emys*] *marmorata*) on Trinity River, Trinity County, California. Carapace length (CL) was compared for adult (>125 mm CL), the upper decile (largest 10% by CL), and younger (2–8 yr) turtles. Data were grouped into three factors of interest for analyses; river fork (free-flowing South Fork [SF] and managed Main Fork [MF]), decade (1990s = 1991–4; 2000s = 2005–7), and by sex for adults > 125 mm CL (female; male), or by age for turtles 2–8 yr old. Relative mass (RM) and volumetric body condition index (vBCI) were compared for adult turtles (>125 mm CL) captured in July or August; vBCI was assessed only for the 2000s and was separated by month (July or August).

	MF 1990s			SF 1990s			MF 2000s			SF 2000s		
	CL	SE	*n*	CL	SE	*n*	CL	SE	*n*	CL	SE	*n*
Adult (>125 mm)												
Female	145.6	1.43	84	164.9	1.93	46	143.3	2.39	30	164.9	1.21	118
Male	151.6	1.52	74	164.1	2.15	37	148.5	2.52	27	166.4	1.53	73
Upper decile												
Female	163.0	0.86	10	184.3	1.57	3	159.9	1.03	7	184.3	0.7	15
Male	169.0	1.11	6	187.3	1.57	3	164.1	1.22	5	189.9	1.03	7
Age (2–8 yr)												
2	52.0	8.15	2	80.1	2.88	16	64.3	5.76	4	78.1	2.26	26
3	70.0	6.65	3	105.6	3.84	9	71.3	5.76	4	100.4	1.82	40
4	93.1	3.84	9	113.6	4.36	7	78.5	4.70	6	114.2	2.10	30
5	98.0	3.47	11	127.0	5.76	4	79.4	3.84	9	125.2	2.64	19
6	94.4	3.84	9	128.2	3.20	13	84.5	3.20	13	126.9	3.33	12
7	114.4	4.36	7	136.7	6.65	3	91.0	2.88	16	141.5	3.84	9
8	118.4	4.07	8	133.5	8.15	2	97.5	2.18	28	143.2	4.36	7
			49			54			80			143
	RM	SE	*n*	RM	SE	*n*	RM	SE	*n*	RM	SE	*n*
RM (residual index)												
Female	0.029	0.004	88	0.031	0.005	50	−0.008	0.004	100	−0.014	0.003	213
Male	0.021	0.004	82	0.048	0.006	32	−0.014	0.004	629	−0.011	0.003	103
							vBCI	SE	*n*	vBCI	SE	*n*
vBCI (volumetric)												
Female-Jul	–	–	–	–	–	–	1.09	0.0169	11	1.01	0.0068	68
Female-Aug	–	–	–	–	–	–	1.09	0.14	16	1.02	0.0089	39
Male-Jul	–	–	–	–	–	–	1.07	0.0169	11	1.04	0.0087	41
Male-Aug	–	–	–	–	–	–	1.08	0.0155	13	1.05	0.0135	17

on the South Fork in the 1990s and 15.2% greater in the 2000s (Fig. 3). For this subset of the largest turtles, there was a significant interaction between fork and decade ($F_{1,55}$ = 10.10, P < 0.0001; Fig. 3). Main Fork females showed a 1.9% decrease in mean CL across the decade, but there was no

Fig. 3. Mean maximum carapace lengths (CL) for the upper decile of males (*n* = 21) and females (*n* = 35) by fork and decade. Error bars are 95% confidence intervals. Numbers on bars are sample sizes.

change in South Fork females; whereas, Main Fork males had a 2.9% decrease in length, but on the South Fork showed a 1.4% increase across the decade (Table 1).

Young turtles (2–8 yr) had significantly greater CLs on the South Fork compared to those on the Main Fork in both the 1990s ($F_{1,325}$ = 353.80, P < 0.0001) and 2000s ($F_{1,325}$ = 27.56, P < 0.0001; Fig. 4). Mean carapace length of young turtles on the South Fork remained relatively constant across the decade, whereas the Main Fork showed a significant decline in size for the same age turtles across the decade (fork x decade; $F_{1,325}$ = 36.29, P < 0.0001; Fig. 4). In both the 1990s and 2000s young turtles on the South Fork had a greater annual increase in CL compared to their Main Fork counterparts (fork x decade, $F_{1,325}$ = 36.29, P < 0.0001). The growth trajectory remained stable on the South Fork across the decade, while growth declined on the Main Fork, with the slopes on the two forks differing significantly (Fig. 5).

Body condition.—There was no difference in mean relative mass (RM) for adult female turtles on the Main Fork compared to those on the South Fork ($F_{1,432}$ = 0.19, P = 0.660; Table 1). Males, however, showed significantly higher mean RM on the South Fork ($F_{1,271}$ = 10.66, P = 0.001; Fig. 6). The difference between decades was much greater than the difference between forks for both females ($F_{1,432}$ =

Fig. 4. Mean carapace length (CL) of turtles 2–8 years (based on photo-corrected annuli counts) by fork and decade. Error bars are 95% confidence intervals.

99.45, $P < 0.0001$) and males ($F_{1,271} = 104.53$, $P < 0.0001$; Fig. 6). For males there was a significant interaction between fork and decade ($F_{1,271} = 6.56$, $P = 0.011$), with the South Fork males showing higher mean RM values in both decades, although this difference was reduced in the 2000s. There was not a significant interaction between fork and decade for females ($F_{1,432} = 0.99$, $P = 0.320$).

The volumetric body condition index (vBCI) of turtles captured in the 2000s indicated that Main Fork turtles had a higher mean vBCI than those on the South Fork (Table 1); the difference between the forks was greater for females ($F_{1,133} = 31.66$, $P < 0.0001$) than males ($F_{1,81} = 6.25$, $P = 0.015$; Fig. 7). We found no significant differences in mean vBCI by month for either sex (female, $F_{1,133} = 0.14$, $P = 0.705$; male, $F_{1,81} = 1.13$, $P = 0.290$). Although not statistically significant, but possibly biologically relevant, males on both forks and females on the South Fork had vBCI means that increased from July to August during the three-year period, whereas females on the Main Fork had the highest mean vBCI over the same period and this value did not increase from July to August (Fig. 7).

Reproductive status.—The proportion of gravid females differed between the forks ($F_{1,606} = 37.62$, $P < 0.0001$) as well as across the decade ($F_{1,606} = 9.47$, $P = 0.002$), with females on the South Fork 2.26 times more likely to be gravid relative to the Main Fork in the 1990s, and 8.19 times more likely in the 2000s (Fig. 8). On the South Fork, 34.2%

of females were gravid in the 1990s and 25.4% in the 2000s. On the Main Fork 15.1% of females were gravid in the 1990s and 3.1% in the 2000s (Fig. 8).

DISCUSSION

Goodman (1997) studied two populations of *Actinemys marmorata* (now *A. pallida*; Spinks et al., 2014) in southern California, finding smaller turtles in colder water below a dam; he posited that the differences in size could be a result of differences in prey availability or water temperature. Lubcke and Wilson (2007) compared populations of *A. marmorata* in the Central Valley of California and found differences in size in three different aquatic habitats, with the smallest turtles at the coldest site, which they attributed to phenotypic plasticity in response to different thermal regimes. Germano and Bury (2009) reported variation in body size among ten lentic and lotic habitats sites in Oregon, which they presumed represented different thermal regimes, but they found no consistent pattern. Bondi and Marks (2013) found significant size differences in *A. marmorata* on the Mad River in northwestern California; however, they found turtles were smaller above rather than below a dam. They attributed this result to intermittent flows above the dam reducing aquatic foraging time during the growing season.

In our study of the two major forks of the Trinity River, each with a unique summer thermal regime, we saw

$CL = (64.13) + (11.21) * (Age)$
$r^2 = 0.702$

$CL = (65.53) + (10.53) * (Age)$
$r^2 = 0.626$

$CL = (50.68) + (8.65) * (Age)$
$r^2 = 0.599$

$CL = (54.08) + (5.34) * (Age)$
$r^2 = 0.474$
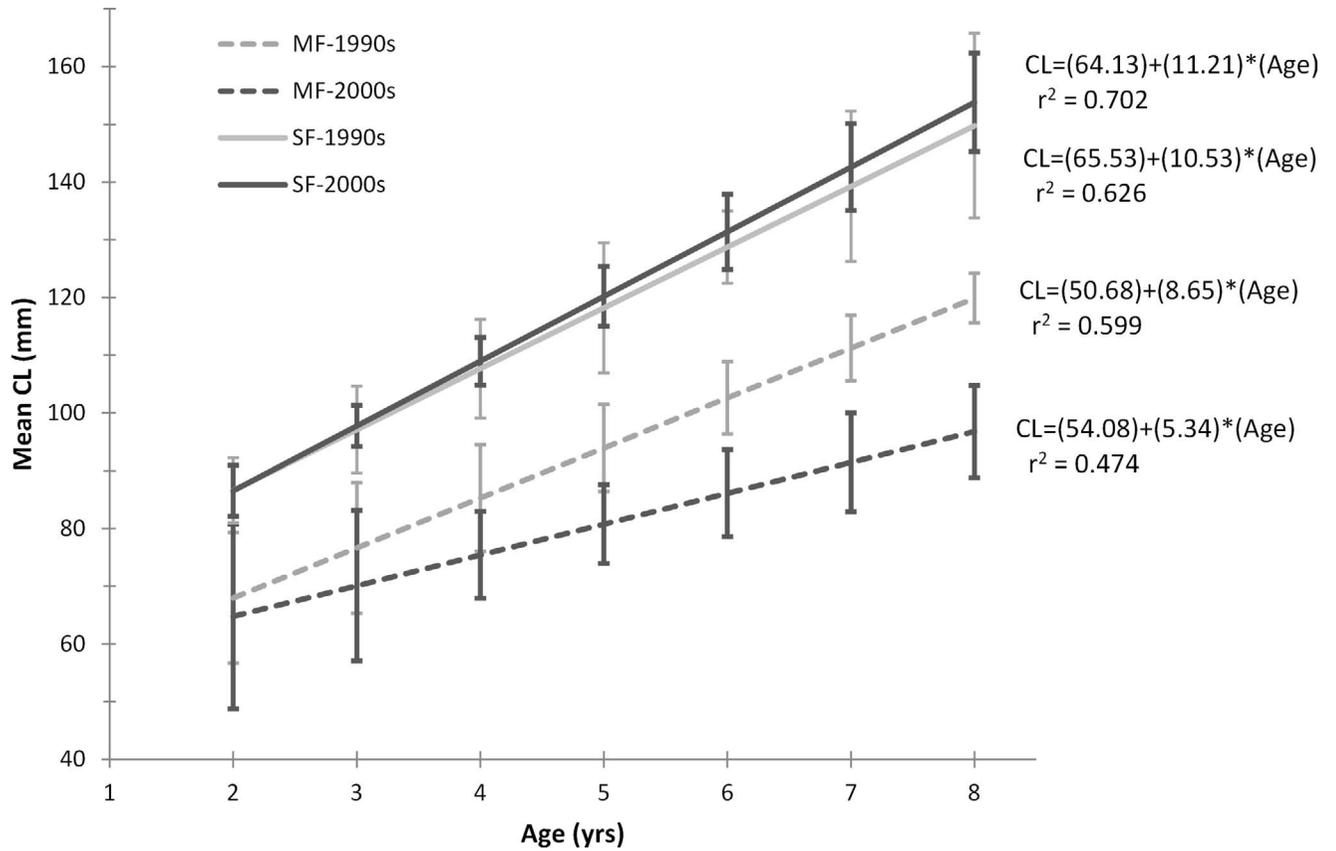
Fig. 5. Regressions of growth of young turtles (2–8 yr) by fork and decade based on a linear growth model.
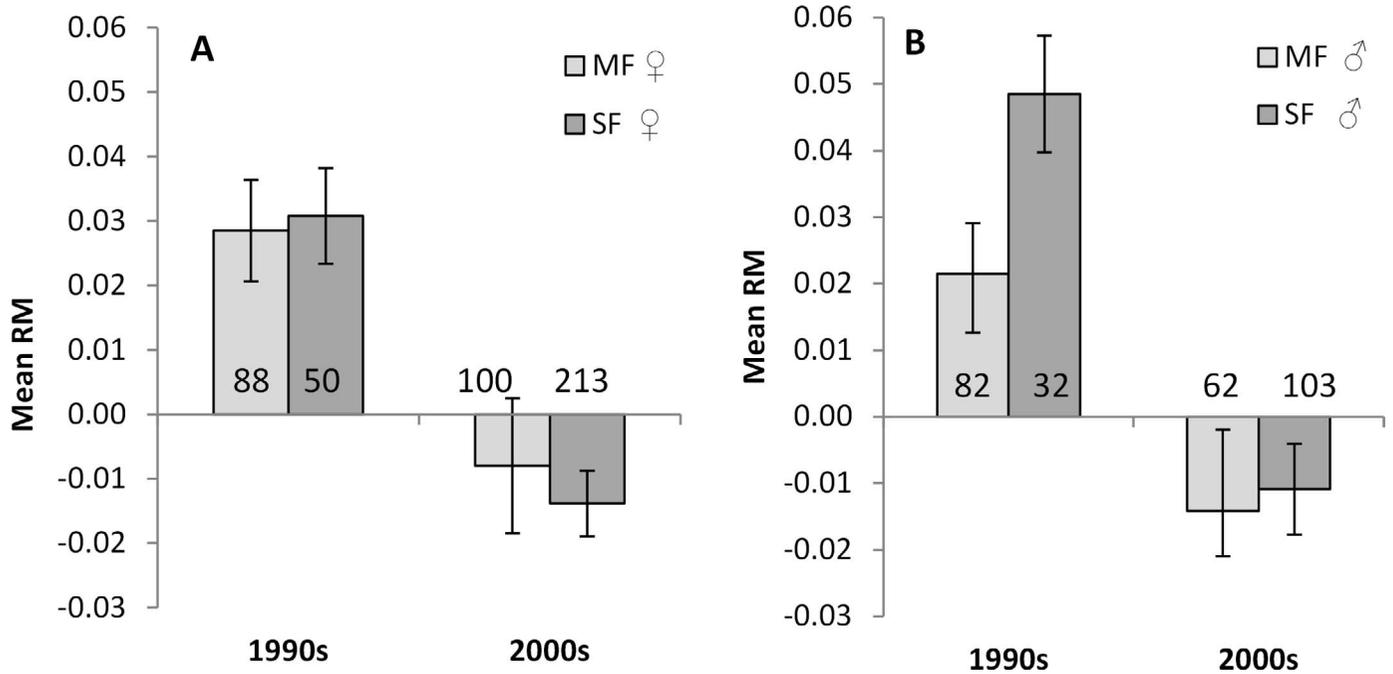
Fig. 6. Relative mass (RM) of turtles > 125 mm CL for: (A) females and (B) males, comparing forks and decade. MF = Main Fork, SF = South Fork. Error bars are 95% confidence intervals.
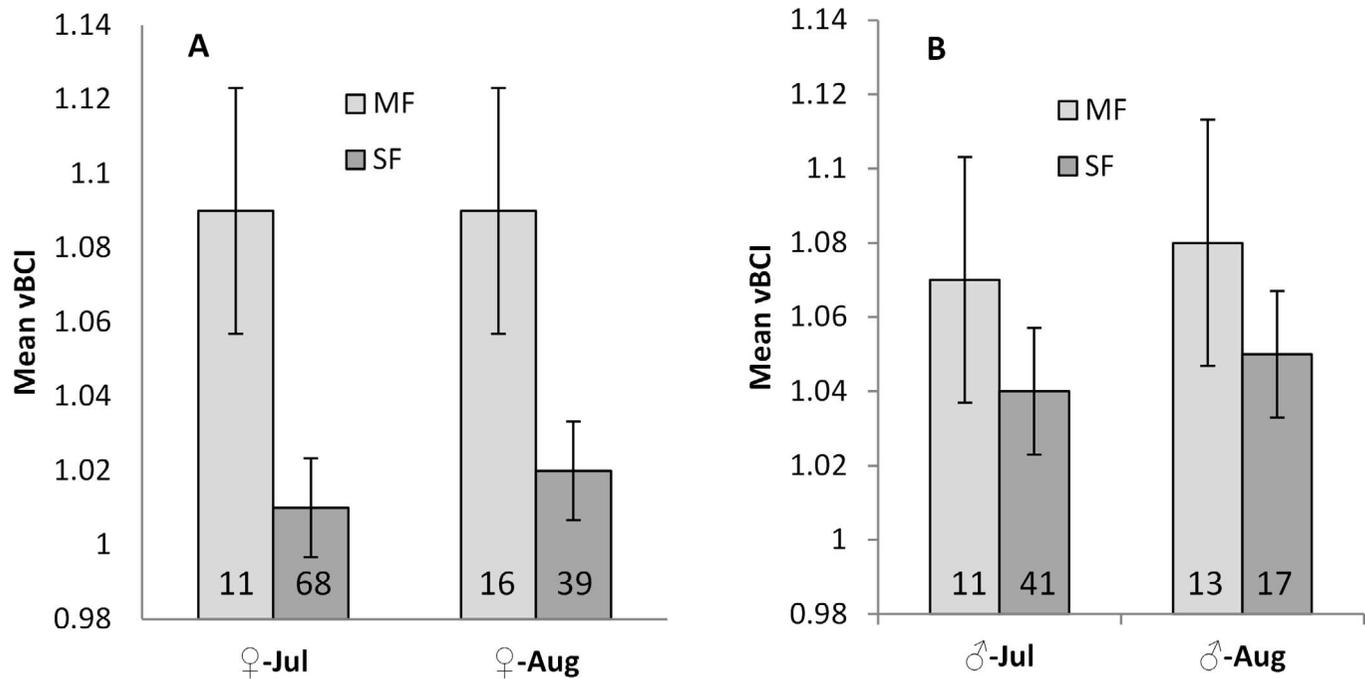
Fig. 7. Volumetric body condition indices (vBCI) of adult turtles captured in July and August from 2005–2007 on each fork. MF = Main Fork, SF = South Fork. Sexes were analyzed separately: (A) female, (B) male. Error bars are 95% confidence intervals. Numbers on bars are sample sizes.

population-level differences in body size consistent with the thesis that the size differences resulted from lower temperatures during the growing season on the regulated Main Fork where July water temperatures averaged 8.6°C colder than on the unregulated South Fork. Our results support the hypothesis that the colder water temperatures during the active season of these turtles is differentially influencing the allocation of resources used for growth and reproduction on the Main Fork compared with the South Fork. In an analysis of female age at maturity based on the data collected during this study, Snover et al. (2015) found a significant correlation between water temperature and growth rate among four reaches, three on the Main Fork and one on the South Fork.

The comparison of carapace lengths (CL) of adults between the two forks indicated a declining trend in average body size of adult turtles on the Main Fork across the decade, a trend not apparent on the South Fork. Of the largest turtles

Fig. 8. The number of gravid and non-gravid females captured by fork and decade. The percentage of gravid females is indicated above each bar. Numbers within bars are sample sizes. MF = Main Fork, SF = South Fork.

in each population (upper decile, presumably the oldest turtles), turtles on the Main Fork were significantly smaller than those on the South Fork. Pond turtles are long-lived (Bury et al., 2012), and it is possible that some individuals on either fork could be older than the dam. In fact, we found some individuals on the Main Fork that exceeded 160 mm CL; however, the proportion of the population represented by these large turtles declined from 14% in the 1990s to 7% in the 2000s. In contrast, on the South Fork the proportion of large turtles (>160 mm CL) increased across the decade from 50% in the 1990s to 60% in the 2000s. We believe the declining numbers of larger (=older) turtles on the Main Fork across the decade is consistent with the thesis that these large individuals are members of a diminishing generation that pre-dates the dam. The increase in number of large turtles on the South Fork appears to evidence a more favorable environment for growth and survival to older ages. We acknowledge that the difference in the proportions of older turtles could be explained by increased recruitment of young turtles on the Main Fork, but this is contrary to the findings of Reese and Welsh (1998a), who found reduced recruitment of young turtles. Furthermore, there could be ecosystem level differences other than the thermal regime that are negatively affecting Main Fork turtles such as a reduced prey base. However, reduced prey would manifest in turtles in poor condition, a fact that was not evident in our RM and vBCI analyses.

Further evidence supporting our hypothesis of thermal regime differences as the causative factor for the observed changes in life-history attributes is found with the young turtles of a known age (2–8 yr). The growth trajectories of the 2–8 yr old turtles reflect the most recent conditions for somatic development, and those on the Main Fork were smaller and showed less annual growth than the comparably aged turtles on the South Fork. The differences between the forks were even more pronounced in the 2000s, suggesting an accelerating trend of restricted growth in the
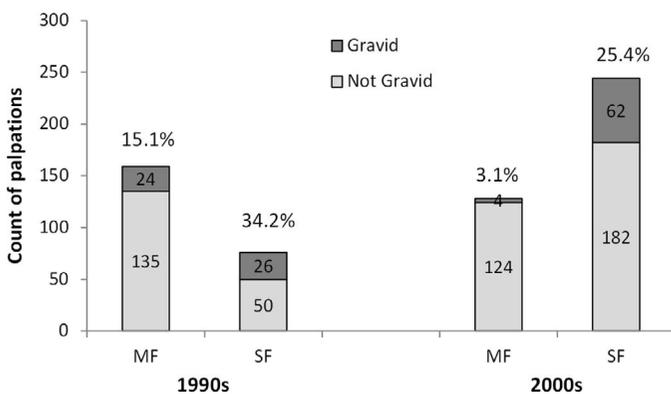
Main Fork turtle population following the Record of Decision (USDI, 2000), a management change that resulted in an increased volume of hypolimnetic releases. In contrast, size and growth rates remained stable on the South Fork across the decade. Snover et al. (2015) compared juvenile growth rates for three reaches along the Main Fork and found a positive relationship between water temperature and annual growth rate.

The size and growth rate differences between the forks also support the hypothesis that the reduced growth rate on the Main Fork is a response to the altered thermal regime and the concomitant loss of warm-water juvenile rearing habitats along the channelized run below the dam (Reese and Welsh, 1998b; Snover et al., 2015). Temperature influences growth and development in a wide range of ectotherms (Atkinson, 1996), and adult body size in turtles may be strongly influenced by their growth rate as juveniles (Gibbons, 1967; Galbraith et al., 1989). Similar variations in growth rates have been attributed to differences in thermal regimes in a number of other turtle species (e.g., Galbraith et al., 1989; Frazer et al., 1991).

The effects of colder temperatures on stream productivity (e.g., a reduction in food availability; Catenazzi and Kupferberg, 2013) may further reduce rate of growth and limit maximum body size potential. In a comparative study of sympatric Painted Turtle (*Chrysemys picta*) populations, Gibbons (1967) reported rapid growth in an artificially heated habitat (nuclear reactor effluent), and later suggested that the increased growth in those populations may have been a result of higher production of lower trophic levels rather than direct temperature effects on turtle physiology (Gibbons, 1970). The influences of proximate mechanisms and their synergisms, and the ultimate long-term population-level impacts of such thermal alterations need to be further explored. Artificially reduced thermal regimes can have unanticipated ecosystem effects. Colder waters (Clarkson and Childs, 2000; Robinson and Childs, 2001) and altered flow regimes (Korman et al., 2005) have both been documented to slow growth in fishes. This response may be both physiological and behavioral as well as a result of reduced resource availability (i.e., limiting foraging time and limited forage). Further, we found evidence supporting the hypothesis that the cold water regime is having a negative influence on the behavior of the Main Fork turtle population based on differences we observed in basking, with individuals on the Main Fork spending more time out of the water basking than those on the South Fork, presumably as compensation for life in colder water (Bettaso et al., unpubl. data).

Our finding of no difference in relative mass (RM) between forks for female turtles whereas males showed a significant difference indicates that females and males were responding differently, with females possibly devoting resources to reproduction over growth. Additional support for the hypothesis that the colder thermal regime is influencing the relative condition of the turtles on the Main Fork comes from the vBCI analysis where both females and males on the Main Fork had significantly higher vBCI values then those on the South Fork. Furthermore, vBCI values for females on the Main Fork were stable across two summer months (July and August), while males on both forks, and females on the South Fork, all showed slight, but not statistically significant, increases in vBCI over this same period. We believe the higher vBCI values for the Main Fork

turtles does not necessarily indicate these turtles are in better health (e.g., Polo-Cavia et al., 2010), but rather they are displaying a physiological response to the altered thermal regime by storing additional resources.

The turtles on the Main Fork showed a pattern of reduced size over the course of this study, with the evidence indicating this is a response to the colder water temperatures on the regulated fork. Ashton and Feldman (2003) found that 19 of 23 chelonian species followed Bergmann's rule, increasing in size with increasing latitude and elevation (=lower temperatures and shorter growing seasons). Contrary to the evolutionary pattern found by Ashton and Feldman (2003), our study is an example of human-induced phenotypic change resulting from the managed flow regime that pushes selection for size in the opposite direction (see also Wolak et al., 2010; Snover et al., 2015).

Life-history theory is based on the concept that trade-offs exist in the allocation of resources. The same energy cannot simultaneously fuel growth and reproduction or simultaneously increase size and number of offspring (Stearns, 1992; Roff, 2002). We suspect that higher mortality of the turtles that have to cope with foraging and predator avoidance in the colder water of the Main Fork may explain the differences in the allocation of resources found on the two forks. Under environmentally challenging conditions, energy resources can be diverted to storage as opposed to growth (Kozlowski et al., 2004) or immediate reproduction (Rollinson and Brooks, 2007). Kozlowski et al. (2004) noted that under high mortality the temperature effect on life histories is just the reverse of that observed with low mortality (i.e., the temperature size rule; Ashton and Feldman [2003], where body size increases in colder clines). Because organisms are constantly selected for maximization of their reproductive output, allocation models can explain the adaptiveness of the decrease in size with lower temperatures (Kozlowski et al., 2004); this would explain the maturity at smaller sizes for turtles on the Main Fork. Further, higher mortality would also explain the selection for greater vBCI values in both sexes on the Main Fork as those with lesser values would be more likely to be removed from the population. The capture of fewer gravid females along with higher and more stable vBCI values on the Main Fork supports the notion that these turtles are diverting resources to storage, possibly for future reproductive efforts, over growth in response to the more challenging thermal regime of the Main Fork. A preliminary analysis of corticosteroid levels revealed a pattern indicative of chronic stress in turtles on the Main Fork but not the South Fork (M. Shultz, unpubl. data), suggesting that Main Fork turtles may be experiencing thermal stress (e.g., Narayan and Hero, 2014).

Body size is a highly heritable character that influences a variety of reproductive fitness components (Stearns, 1992; Roff, 2002). Turtles are susceptible to changes in reproductive fitness that could lead to population declines because of their unique life-history characteristics of delayed sexual maturity, long life span, low reproductive rate, and strong site fidelity (Congdon et al., 1993; Seigel and Gibbons, 1995; Tucker et al., 2001). Our data indicated that the average size of turtles on the Main Fork has been declining over at least a decade, and probably longer, following alterations of the natural flow and thermal regimes. Consequently, the average clutch size or egg size, or both (Roosenburg and Dunham, 1997), may also have declined; lower reproductive

output ultimately reduces population size (e.g., Ligon and Stacey, 1996; Brooks et al., 1999; Hossack et al., 2013).

How a species responds to environmental disturbance depends on the type and magnitude of disturbance, the amounts and configuration of remaining habitats, and their life-history characteristics (Prugh et al., 2008; Kuussaari et al., 2009). The spatial scale of a disturbance relative to the spatial distribution of the population is important because it determines how fitness is estimated when modeling their life-history evolution (Lytle, 2001). The altered thermal regime from the damming of the Main Fork Trinity is a landscape scale disturbance because it has permanent influence on all downstream aquatic habitats with hydrologic links to the main channel. The alterations to the thermal and physical characteristics of this lotic ecosystem, because they affect the entire population of the Main Fork and the preponderance of riverine aquatic habitats, would be characterized as a chronic coarse-grained disturbance with negative evolutionary implications for this turtle population (Iwasa and Levin, 1995). As a result, the geometric mean of reproductive success over multiple seasons, the appropriate measure of population fitness (Lytle, 2001), is most likely declining in the Main Fork turtle population, indicating a long-term loss of viability (Kuussaari et al., 2009).

There were pronounced changes across the decade apparent on both forks. The BCI of both sexes changed from positive in the 1990s to negative in the 2000s, and we detected fewer gravid females during the 2000s relative to the 1990s. While we did not collect evidence that would allow us to discern the reasons for these dramatic shifts, a decline in two metrics of fitness (RM and reproductive output) of these turtle populations indicated reduced fitness across this entire region. Our observations suggest a need for further investigations into what may be altering the timing or output of primary and secondary productivity in the trophic web upon which these turtles depend. Negative impacts to trophic interactions have been attributed to the influence of global warming in similar ecosystems (e.g., Petchey et al., 1999; Emmerson et al., 2005; Kratina et al., 2012; Ockendon et al., 2014).

Actinemys marmorata is long-lived, so traditional studies of population status associated with disturbance are difficult, and it could take decades to see effects. This study looked at indicators of population health and provided evidence that alteration of flow and thermal regimes by damming have had significant and long-term effects on growth and reproduction of these turtles. We acknowledge that size, growth, body condition, and reproductive output can be influenced by genetic, climatic, and biotic factors; however, the proximity of these populations, presence of a few large, presumably older individuals on the Main Fork, and evidence for behavioral differences (Bettaso et al., unpubl. data) support the more parsimonious interpretation that the profound differences in these two populations are the result, at least in part, of the differences in the flow and thermal regimes that are the outcome of flow management. This trend could be mitigated by re-establishing the natural regimes under which this population has evolved (Olden and Naiman, 2010; Kiernan et al., 2012). Increased channel complexity including enhanced shallow-edge and backwaters can provide thermal diversity without compromising fisheries objectives for cold summer water. Restoration efforts that promote habitat heterogeneity have the best chance of promoting multiple species (Biebighauser, 2007). Sustaining native biodiversity and related processes (i.e., food web dynamics) in managed riverine systems is challenging; however, it is the only approach likely to assure that natural, self-sustaining ecological and evolutionary processes are retained in these systems (Palmer, 2009; Palmer et al., 2010; Naiman et al., 2012).

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Appendix 1. Body mass and morphometric measurements. Body mass was measured with Pesola spring scales to the nearest 1.0 g for turtles >100 g, and to the nearest 0.1 g for those <100 g. Shell morphometrics were measured as straight line distance with calipers to the nearest millimeter for larger turtles (>150 mm carapace length), and to the nearest 0.1 mm for smaller turtles (<150 mm CL). Columns to the right indicate measurements recorded in each study period (Yes/No/Incomplete).

Measurement	Technique	Study period 1990s	Study period 2000s
Carapace length	Straight-line distance:		
Maximum (CL)	Greatest anterior to posterior span, parallel to midline; 1st or 2nd marginal to 12th marginal; either side	Y	Y
Minimum (cl)	Mid-line at posterior to cleft between nuchal and 1st marginal; either side	I	Y
Width (Cwd)	Perpendicular to axis; suture between 2nd and 3rd vertebral shield	N	Y
Plastron length	Straight-line distance:		
Maximum (PL)	Greatest anterior to posterior span, parallel to midline; gular to anal shield; either side	N	Y
Minimum (pl)	Plastron mid-line	N	Y
Width (Pwd)	Suture between abdominal and femoral shields; at posterior edge of the bridge	N	Y
Shell height (SH)	Maximum dorso-ventral span	N	Y
Mass	Pesola spring scale:		
1990s	Scale clipped to plastic baggie	I	N
2000s	Scale clipped to rubber band belt	N	Y