

Evidence of counter-gradient growth in western pond turtles (*Actinemys marmorata*) across thermal gradients

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SUMMARY

1. Counter-gradient growth, where growth per unit temperature increases as temperature decreases, can reduce the variation in ectothermic growth rates across environmental gradients. Understanding how ectothermic species respond to changing temperatures is essential to their conservation and management due to human-altered habitats and changing climates.

2. Here, we use two contrasting populations of western pond turtles (*Actinemys marmorata*) to model the effect of artificial and variable temperature regimes on growth and age at reproductive maturity. The two populations occur on forks of the Trinity River in northern California, U.S.A. The South Fork Trinity River (South Fork) is unregulated, while the main stem of the Trinity River (Main Stem) is dammed and has peak seasonal temperatures that are approximately 10 °C colder than the South Fork.

3. Consistent with other studies, we found reduced annual growth rates for turtles in the colder Main Stem compared to the warmer South Fork. The South Fork population matured approximately 9 year earlier, on average, and at a larger body size than the Main Stem population.

4. When we normalised growth rates for the thermal opportunity for growth using water-growing degree-days (GDD), we found the reverse for growth rates and age at reproductive maturity. Main Stem turtles grew approximately twice as fast as South Fork turtles per GDD. Main Stem turtles also required approximately 50% fewer GDD to reach their smaller size at reproductive maturity compared to the larger South Fork turtles.

5. We found we could accurately hindcast growth rates based on water temperatures estimated from the total volume of discharge from the dam into the Main Stem, providing a management tool for predicting the impacts of the dam on turtle growth rates.

6. Given the importance of size and age at reproductive maturity to population dynamics, this information on counter-gradient growth will improve our ability to understand and predict the consequences of dam operations for downstream turtle populations.

Keywords: counter-gradient growth, phenotypic plasticity, western pond turtle

Introduction

An understanding of somatic growth rates, including their variability and the influence of changing environmental conditions, is fundamental to the study of size-structured population dynamics (Heppell, Snover & Crowder, 2003; Armstrong & Brooks, 2013; Avens &

Snover, 2013). Growth rates govern key life-history variables including age and size at reproductive maturity, survival to reproductive maturity and size-specific fecundity (Stearns & Koella, 1986; Willemsen & Hailey, 2001; Day & Rowe, 2002; Walters & Hassall, 2006). As a taxonomic group, turtles generally have slower juvenile growth rates and delayed age at reproductive maturity

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in comparison to other similar-sized ectotherms (Scott, Marsh & Hays, 2012), making their growth rates particularly relevant to both life-history theory (Stearns & Koella, 1986; Shine & Iverson, 1995) and their conservation (Crowder *et al.*, 1994; Willemsen & Hailey, 2001; Heppell *et al.*, 2008).

For ectotherms, environmental temperature drives much of the variability in size-at-age and growth rates (Adolph & Porter, 1993; Brown *et al.*, 2004). Therefore, because growth rates drive key life-history traits in ectotherms, by extension temperature can drive life-history traits and ultimately population production (Neuheimer & Taggart, 2007). Growing degree-days (GDD) have recently gained traction as a method for explaining time- and temperature-dependent variation in fish growth and development (Neuheimer & Taggart, 2007; Rypel, 2012b; Chezik, Lester & Venturelli, 2014) and for detecting counter-gradient growth patterns where growth per unit temperature increases as temperature decreases (Power & McKinley, 1997; Venturelli *et al.*, 2010; Rypel, 2012a). Growing degree-days have been used extensively in agriculture, plant biology and entomology as predictors of growth and development, and have been applied to an increasing number of fish studies (e.g. Neuheimer, Taggart & Frank, 2008; Neuheimer & Grønkvær, 2012; Rypel, 2012b; Chezik *et al.*, 2014). Its application to other ectothermic vertebrates such as reptiles has been limited and generally focused on terrestrial species (Zani & Rollyson, 2011).

As with other ectotherms, temperature is a key environmental factor influencing rates of metabolism and locomotor function (Ben-Ezra, Bulté & Blouin-Demers, 2008), as well as juvenile growth rates and time to maturity in turtles (Frazer, Greene & Gibbons, 1993). Western pond turtles (*Actinemys marmorata*) rely primarily on aquatic habitats for foraging, mating, predator escape and rest. Like other emydid turtles, they also rely heavily on aerial basking as a means of thermoregulation (Bury *et al.*, 2012a). While basking turtles can achieve substantially higher body temperatures compared to water temperatures, once resubmerged, body temperatures rapidly reach equilibrium with the water due to its high thermal conductivity (Ben-Ezra *et al.*, 2008). Hence, it is possible that water-growing degree-days (GDD) may be a viable metric for explaining variation in size-at-age using methods similar to those employed in fish studies (Neuheimer & Taggart, 2007). This approach may be especially useful in studying and anticipating the impacts of anthropogenically induced changes in thermal regimes, which can happen over a relatively short period of time in an evolutionary context (Isaak

et al., 2012). Dam-controlled river systems are an example of anthropogenically induced rapid local changes in thermal regimes. The prevalence of dammed river systems, and the subsequent change in temperature regimes, has dramatically altered many riverine communities downstream of dams (Clarkson & Childs, 2000; Olden & Naiman, 2010).

Understanding turtle growth rates is complicated by a lack of size-at-age information for large and/or old turtles due to difficulties in assigning age using common methods of scute mark counts or skeletochronology (Bury & Germano, 1998; Snover & Rhodin, 2007). Previous growth models for turtles in general, and western pond turtle specifically, have compensated for this lack of data by setting the asymptotic size parameter as a constant based on size distributions of adult turtles (Germano & Rathbun, 2008; Germano & Bury, 2009; Bury, Germano & Bury, 2010; Germano, 2010; Piovano *et al.*, 2011). This approach has a drawback of not allowing the data to inform asymptotic size patterns, which can be especially problematic in comparing populations (Piovano *et al.*, 2011). Recently, Armstrong & Brooks (2013) presented a somatic growth model that incorporates both size-at-age and growth rate information to estimate growth model parameters for snapping turtles (*Chelydra serpentina*).

Here, we develop somatic growth models using an approach similar to Armstrong & Brooks (2013) for western pond turtles in the Trinity River system to improve our ability to predict the consequences of dam operation and other factors that change thermal regimes. We use the models to detect population differences in female growth trajectories and age at reproductive maturity between two populations of western pond turtles. One population occurs in the unregulated South Fork Trinity River (South Fork), while the other population occurs in the dammed main stem of the Trinity River (Main Stem; Reese & Welsh, 1998a,b; Ashton, Bettaso & Welsh, 2015). The Main Stem experiences controlled hypolimnetic flows from the dam, maintaining a thermal regime that is colder than normal for the region. The South Fork maintains a natural thermal regime and is a tributary of the Main Stem, with the confluence 65 km below the confluence with the North Fork Trinity River (Fig. 1).

Methods

Species and study area

Western pond turtles are omnivorous predators and scavengers (Bury, 1986) inhabiting a variety of aquatic

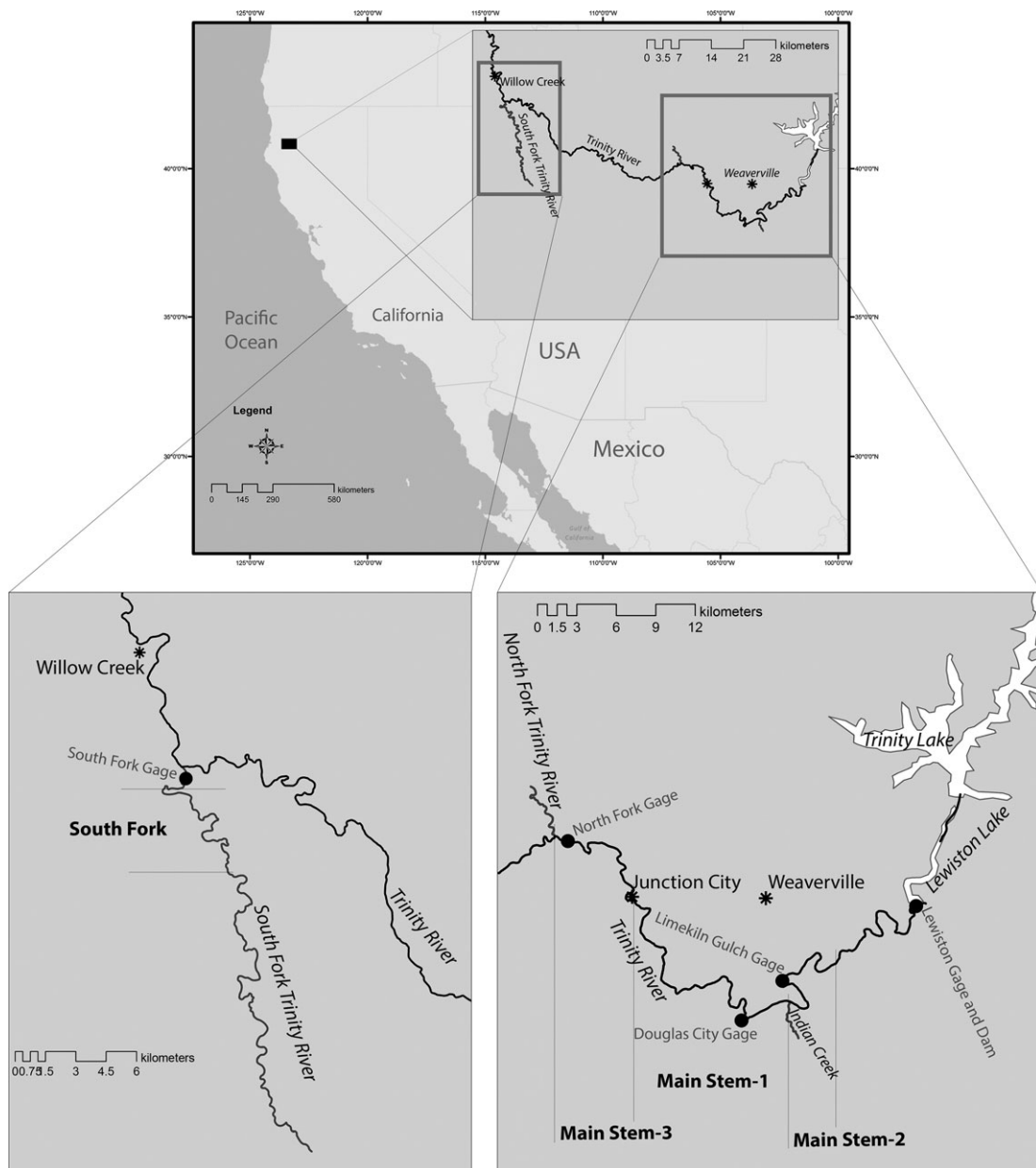


Fig. 1 Location of western pond turtle (*Actinemys marmorata*) study area in Trinity County, California, U.S.A. Solid black line is the main stem of the Trinity River, dark grey lines are tributaries of the river, Trinity and Lewiston Lakes are shown in white, and asterisks denote townships. Enlargements of study area maps (lower panels) show river segments (breaks denoted by straight gray lines) where turtle captures occurred. South Fork, Main Stem-1, Main Stem-2 and Main Stem-3 denote the data set names for captures from each segment (see Table 1). Filled black circles are the locations of stream gages for water temperature or flow rates (Lewiston, USGS Code: 11525500; Limekiln, USGS Code: 11525655; Douglas City USGS code: 11525854; North Fork, USGS code: 11526400; and South Fork, Trinity River Restoration Program Online Data Portal; <http://odp.trrp.net/TSA/TSA.aspx>). Not shown is the Hyampom gage (USGS Code: 11528700) upstream of the South Fork segment on the South Fork Trinity River.

habitats during their active season, including rivers, streams, lakes, ponds, reservoirs and wetlands (Bury *et al.*, 2012a). They also make extensive use of terrestrial habitats for nesting and over-wintering (Reese & Welsh, 1997; Pilliod, Welty & Stafford 2013). Their distribution is limited to chiefly west of the Sierra-Cascade crest

along the Pacific coast of North America, from Baja California, Mexico, to Washington, U.S.A. (Bury *et al.*, 2012b). Recently, a study on their population genetics suggests that populations south of the San Francisco Bay area are a separate species, *Actinemys pallida* (Spinks, Thomson & Shaffer, 2014). Mature females produce one

to two clutches of eggs per year, depositing them in excavated terrestrial nests between May and July; however, not all females will reproduce every year (Scott *et al.*, 2008; Bury *et al.*, 2012b). In more northern latitudes, including our study area, hatchlings overwinter in nests and emerge the following spring (Reese & Welsh, 1997; Rosenberg & Swift, 2013). Very little data exist on the average lifespan for western pond turtles; however, Bury *et al.* (2012a) report that some turtles are known to live at least 55 year based on recapture data.

Western pond turtles inhabit the Trinity River system in Trinity County, California, U.S.A. (Fig. 1; Reese & Welsh, 1998a,b; Ashton *et al.*, 2015). The construction of two dams, an upper (Trinity) and a lower (Lewiston), on the Main Stem was completed in 1964. While a small power plant is operated by the Trinity Dam, the main purpose of regulating the river is to provide water for agriculture to the Central Valley of California (US Fish and Wildlife Service and Hoopa Valley Tribe 1999). The result of the dams, combined with subsequent flooding events and water control actions, was a severely modified channel, with an estimated loss of 80–90% of fishery habitat for the native salmon and steelhead populations (Department of the Interior, 2000). Efforts to rehabilitate the river began in 1980 and continue today with the efforts led by the interagency Trinity River Restoration Program (Department of the Interior, 2000). Currently, there are minimum mandated flows year-round, and spring hydrographs for dam releases are determined based on water year types, with less water released during dry years (Department of the Interior, 2000). Management of the river includes water temperature targets designed to protect the native salmonids. Flow into Lewiston Lake, and consequently the Trinity River, is hypolimnetic from Trinity Dam and remains a relatively constant 9 °C throughout the summer in most years (Department of the Interior, 2000). This water temperature is maintained by flow releases from the Trinity Lake above the Trinity Dam into Lewiston Lake. Trinity Lake is a large, deep lake that remains thermally stratified throughout most of the summer, with some exceptions in very dry years. When agricultural water diversions are large, flow from the cold Trinity Lake into Lewiston Lake is relatively constant and Lewiston Lake remains cold. When water diversions are low, Lewiston Lake can begin to warm, which can have negative impacts on the fish hatchery immediately downstream of Lewiston Dam; hence, the warm water is pulsed through the diversion and replaced with Trinity Lake water to maintain cold Lewiston Lake water temperatures and hence Trinity River

temperatures, throughout the growing season (US Fish and Wildlife Service and Hoopa Valley Tribe 2000). The steady influx of cold water makes mean summer water temperatures artificially low for rivers in this region. In contrast, the South Fork maintains its natural flow and temperature characteristics with summer water temperatures reaching 24 °C. The two rivers are otherwise climatologically similar (Reese & Welsh, 1998a,b; Ashton *et al.*, 2015).

The study site on the Main Stem consisted of a 63-km stretch between the Trinity/Lewiston Dams and the confluence with the North Fork Trinity River (Fig. 1). The study site on the South Fork was an 8.6-km reach between 9.0 and 0.4 km above the confluence with the Main Stem (Fig. 1; see Reese & Welsh, 1998a,b; Ashton *et al.*, 2015 for additional details).

Turtle data

Paired mark–recapture studies of western pond turtles have been conducted on the Main Stem and South Fork intermittently from 1991 through 2010, using multiple study designs and addressing different management questions (Reese & Welsh, 1998a,b; Ashton *et al.*, 2015). These studies have resulted in a large database of size-at-age and growth rates spanning nearly two decades. For the growth rate analysis, we used data from any female or any juvenile ≤ 125 mm carapace length (CL) recorded as the maximal straight-line length measured from the outer edge of the first or second marginal scute to the outer edge of the last marginal scute on either side of the midline (Ashton *et al.*, 2012). A carapace length of 125 mm is the minimum size at which secondary sex characteristics begin to appear allowing differentiation of the sexes by visual examination; this length is generally considered a minimum size at maturity for these populations of western pond turtles (Reese & Welsh, 1998a; Ashton *et al.*, 2015). Within this subset of the data, we used only records for turtles that (i) were captured in or along (i.e. shoreline) the main channel for either the Main Stem or South Fork, (ii) had CL recorded and (iii) could be aged reliably based on scute marks (Bury & Germano, 1998), or turtles that were recaptured at least once providing growth rates. We used the difference in length between captures as our measure of growth rate. Because growth rates are not constant year-round, only those where the time between measurement was >11 months were retained.

From these data, we created five data sets corresponding to four portions of our study area and separating decades for the primary Main Stem reach (Fig. 1). The

first two were used for growth model-fitting, but the other three had inadequate data for model-fitting and were only used to provide information on juvenile growth rates for different areas of the Main Stem and between decades. The five data sets were South Fork, Main Stem-1, Main Stem-2, Main Stem-3 and Main Stem-1990 (Fig. 1, Table 1). The first four data sets included all data from 2004 to 2010, while the fifth data set included captures from 1991 to 1996 that could be aged reliably based on scute marks, and where captures occurred in the same area as Main Stem-1 (Table 1). For the Main Stem-1 data set, we also included turtles that were initially captured prior to 2004, had ages assigned at initial capture and were subsequently recaptured between 2004 and 2009. This enhanced our sample of known-aged large turtles in the data set.

Turtle age assignments

When possible, turtles were aged based on annuli counts on plastron scutes (Ashton *et al.*, 2015). Annual deposition of scute marks has been demonstrated for western pond turtles in this region (Bury & Germano, 1998; Germano & Bury, 1998). Annuli cannot be used to estimate age in older turtles due to the following reasons: (i) compression of the growth marks, making them difficult to discern; (ii) wearing of scute marks erases the ridges of early marks. Hence, ages based on scute marks were primarily only available for juvenile turtles.

For western pond turtles in this region, most growth is presumed to occur between April and September. Hence, there can be large differences between the sizes of a given-aged turtle captured in May compared to August, artificially increasing the variability in size-at-age (Venturelli *et al.*, 2010). To account for this seasonal growth, we converted age assignments to seasonal ages starting at 1 April, approximating the timing of the onset of activity, foraging and growth for the season. Age was assigned as the number of years prior to 1 April of the year of capture, plus the fraction of the year between 1 April and the date of capture. We assigned hatchling age in the same manner, letting age zero represent emergences from the nest in the spring, approximated as 1 April. Age 0+ turtles were hatchlings experiencing their first year of growth post-emergence.

Size of gravid females

To determine the smallest size at reproductive maturity for each river, we created a separate data set, restricting the original data (from 1991 to 2010) to positively identi-

Table 1 Abbreviations used for study units and data sets (see Fig. 1 for locations)

Study unit abbreviation	River	Location description
South Fork	South Fork Trinity River	8.6 km between 9.0 and 0.4 km above the confluence with the main stem of the Trinity River
Main Stem	Main stem of the Trinity River	63 km between the Lewiston Dam and the confluence with the North Fork Trinity River
Data sets	Location	Time frame
South Fork	8.6 km between 9.0 and 0.4 km above the confluence with the main stem of the Trinity River	2004–2010
Main Stem-1	On the Main Stem between Indian Creek and Junction City	2004–2010
Main Stem-2	On the Main Stem between Tom Lang Gulch and Indian Creek	2004–2010
Main Stem-3	On the Main Stem between Junction City and North Fork Trinity River	2004–2010
Main Stem-1990	On the Main Stem between Indian Creek and Junction City	1991–1996

fied females >125 mm CL for which reproductive condition was scored as gravid based on palpation (see Ashton *et al.*, 2015 for details). For this analysis, we pooled all Main Stem data. We used two-tailed Student's *t*-tests to compare sizes of gravid turtles between each river. We compare these results to studies of other western pond turtle populations.

Environmental data

Data on water flow and temperatures came from the United States Geological Survey (USGS) National Hydrography Database (<http://waterdata.usgs.gov>). We used data from four stream gages for the Main Stem and two stream gages for the South Fork (Fig. 2). For the Lewiston and Hyampom gages, we summed the average daily flow and report results in total cubic metres of flow per year. Time frames for temperature data used from the other four stream gages were: Limekiln 2001–2008, Douglas City 2000–2008, North Fork 2000–2004 and South Fork 2006–2008.

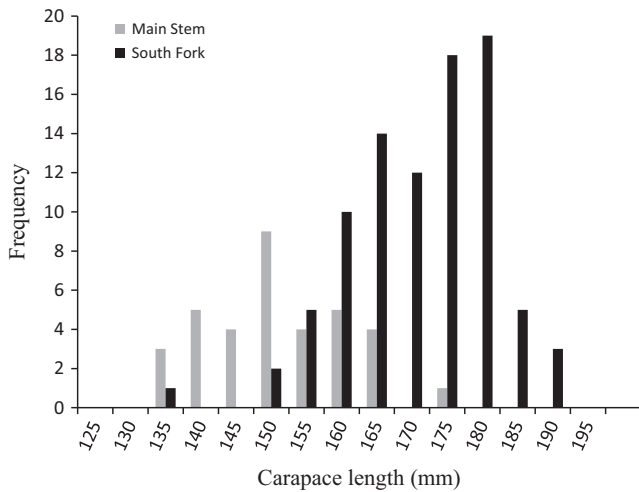


Fig. 2 Size distribution of gravid female western pond turtles (*Actinemys marmorata*) where eggs were detected by palpation. Gray bars represent the main stem of the Trinity River ($N = 35$), black bars represent the South Fork Trinity River ($N = 54$).

Growing degree-days (GDD) were calculated as (Neuheimer & Taggart, 2007)

$$\text{GDD} = \sum_{i=1}^n (T_i - T_0) \quad (1)$$

where n is the number of days (either 365 for GDD year⁻¹ or turtle age in days), T_i is the average temperature on day i , and T_0 is the threshold temperature below which growth does not occur. Numerous studies have found that 10 °C is an approximate lower temperature threshold for activity in reptiles (see Zani & Rollyson, 2011 for review). Hence, we use $T_0 = 10$ °C for this study, and from this point, forward GDD represents the cumulative sum of temperatures above 10 °C. We averaged temperatures for each day of the year across time frames for each gage to estimate average GDD per year. We then converted turtle ages in year (henceforth termed annual age) to age based on the cumulative GDD experienced by each turtle (henceforth termed GDD age). To determine GDD age, we used the mean temperature for each calendar day from the stream gages and summed GDD with time zero starting at 1 April for each turtle age in days.

Growth models

Somatic growth models were fit to the South Fork and Main Stem-1 data sets. We used the following form of the von Bertalanffy growth function for turtles for which age could be confirmed from scute ring counts:

$$\hat{L}_{i,j} = L_{\infty} (1 - \exp(-k(t_{i,j} - t_0))) \quad (2)$$

where $\hat{L}_{i,j}$ is the expected carapace length of individual i at its j th capture, L_{∞} is the asymptotic length, k is a growth coefficient describing the rate at which asymptotic length is reached, $t_{i,j}$ is the age of individual i at the j th capture, and t_0 is the theoretical age at size zero. For marked turtles of unknown age that were recaptured at least once, we used the following equation:

$$\hat{L}_{i,j} = L_{\infty} - (L_{\infty} - L_{i,j}) \exp(-k(y_{i,j+1} - y_{i,j})/365) \quad (3)$$

Here, y indicates the date of capture such that $y_{i,j+1} - y_{i,j}$ is the time between successive captures, measured in days. For both equations, we assumed that the error between actual and expected lengths of individuals i at time of marking or recapture, j , was normally distributed:

$$L_{i,j} = \hat{L}_{i,j} + \epsilon \quad (4)$$

where $\epsilon \sim N(0, \sigma^2)$.

To detect a difference in growth patterns between the South Fork and Main Stem-1 data sets, we compared a full model, assuming that the von Bertalanffy parameters were specific to each population (i.e., $L_{\infty,S}$, $L_{\infty,M}$, k_S , k_M , $t_{0,S}$ and $t_{0,M}$, where S represents South Fork and M represents Main Stem-1) to a reduced model that assumed the von Bertalanffy parameters were common to both habitats (i.e., L_{∞} , k , and t_0). We then tested the assumptions that the individual parameters were either common or specific to each data set, resulting in a total of eight models (see Table 4 in the results section for the parameters used in each model).

We used Bayesian fitting procedures in the program winBUGS to find the joint likelihood of the asymptotic length and rate parameters for equations 3 and 4 for each model (Armstrong & Brooks, 2013). Uninformative priors were assigned to most model parameters and hyperparameters: $k \sim \text{beta}(1,1)$, a beta distribution with the same probability for any values between 0 and 1; $t_0 \sim N(0, 100^2)$, a normal distribution with a mean of 0 and a standard deviation of 100; and $\sigma^2 \sim U(0,100)$, a uniform distribution with the same probability for any values between 0 and 100. For asymptotic length, we used a semi-informative prior based on information about adult-sized turtles, $L_{\infty} \sim N(100, 100^2)$. The same priors were used for the population-specific parameters. All models were run with two chains and checked for convergence using diagnostic tools of Gelman & Rubin (1992). We used chain lengths of 100 000 samples, discarding the first 10 000 as burn-in samples, and did not thin the chains. Hence, parameter inference was made

using 90 000 samples, where the mean and median were used as point estimates and 95% prediction intervals as measures of uncertainty.

To select the most appropriate model for the data, we used deviance information criterion (DIC). To ensure the models were adequately fitting the data, we used posterior simulations (Gelman *et al.*, 2004). In posterior simulations, expected length, as a function of either age (Eq. 2) or initial length (Eq. 3), was simulated using the growth models and random samples of parameters from the joint posterior distribution. We evaluated the probability (P_n), where n is the total number of observations from Table 2, of the observed length occurring in the simulated data (Gelman *et al.*, 2004). We computed P_{95} as the proportion of $P_n > 0.025$ and < 0.975 . Hence, higher values for P_{95} indicate better model fits (Eguchi *et al.*, 2012). We use the best-fitting models to estimate age at reproductive maturity for females from both rivers based on size at reproductive maturity.

Juvenile growth rates

A prior study (Ashton *et al.*, 2015) reports that Main Stem juvenile turtles are smaller at a given age compared to South Fork turtles. We expand their analysis by comparing three segments of the Main Stem that

experience different thermal environments driven by their distance from the dam. We used all four data sets from the 2000s to estimate mean juvenile growth rates in terms of both mm year⁻¹ (termed annual growth rates) and mm• GDD⁻¹ (henceforth termed GDD growth rates). As growth rates are relatively linear for small, young turtles >1 year old (Ashton *et al.*, 2015), we used least-squares linear regression to estimate both growth rates, using data for 1.0- through 7.9-year-old Main Stem turtles. For the South Fork, because growth rates are beginning to slow by age 5, we used data for 1.0- to 4.9-year-olds. We compared the slopes of the regressions using analysis of covariance (ANCOVA) and used Tukey HSD tests for *post hoc* comparisons.

We used the Main Stem-1990 data set to test whether dam releases and GDD can be used to predict juvenile growth rates. We applied the relationship found between GDD at the Douglas City gage and discharge into the Main Stem from the Lewiston Dam to estimate Douglas City GDD during the time frame of the Main Stem-1990 captures (see Results – Environmental data). We then used the relationship found between GDD and GDD growth rates (see Results – Juvenile growth rates) to estimate the annual growth rate predicted by the GDD. We compared the predicted annual growth rate to the value determined from a least-squares linear

Table 2 Sample sizes for western pond turtle (*Actinemys marmorata*) captures for the South Fork (South Fork) Trinity River and the main stem (Main Stem) of the Trinity River, Trinity County, California, U.S.A. Data for the main stem of the Trinity River was partitioned into four subsets (see Fig. 1 for locations): Indian Creek to Junction City (Main Stem-1), Tom Lang Gulch to Indian Creek (Main Stem-2), Main Stem Junction City to the confluence with the North Fork Trinity River (Main Stem-3) and Indian Creek to Junction City (Main Stem-1990). The data sets South Fork, Main Stem-1, Main Stem-2 and Main Stem-3 were limited to captures between 2004 and 2010; the MS 1990 was limited to captures between 1991 and 1996

	Data set				
	South Fork	Main Stem-1	Main Stem-2	Main Stem-3	Main Stem-1990
Total turtles	280	156	8	13	58
Number of known-aged turtles	164	113	8	13	58
Recaptures per known-aged turtle					
0	117	55	8	8	56
1	37	41	0	5	1
2	9	14	0	0	1
3	0	3	0	0	0
4	1	0	0	0	0
Total age records	223	191	8	18	61
Range of carapace lengths (mm)	25.6–157	25.6–158	37.2–83.0	50.2–106.5	51–135
Range of ages (year)	0.1–12.4	0.1–22.3	1.1–7.5	1.2–7.3	1.2–7.4
Recaptures per unknown-aged turtle					
1	73	24	–	–	–
2	35	13	–	–	–
3	6	5	–	–	–
4	2	1	–	–	–
Total growth rates	169	69	–	–	–
Range of carapace lengths (mm)	112.0–187.0	101.1–162.0	–	–	–

regression fit to the Main Stem-1990 juvenile size-at-age data.

Juvenile growth rates and age at reproductive maturity

If western pond turtles grow at the same GDD growth rate regardless of GDD year⁻¹ (Neuheimer & Taggart, 2007), we expect a negative relationship between annual growth rates and the GDD year⁻¹ for each river segment. Similarly, we expect no relationship between GDD growth rates and GDD year⁻¹ for each river segment. We compared these expectations, using the South Fork GDD growth rates for all river segments, to the observed juvenile annual and GDD growth rates. Similarly, we compared our observations of age at reproductive maturity to the assumption of reproductive maturity occurring at the same GDD age for each river.

Results

Turtle data

A summary of sample sizes, age ranges and size ranges for the captured and recaptured turtles is in Table 2.

Size of gravid females

Mean lengths of gravid turtles were significantly smaller for the Main Stem (Fig. 2; 148.8 ± 9.9 mm carapace length (CL), $N = 35$) compared to the South Fork (169.3 ± 9.8 mm CL, $N = 89$; $t = 1.98$, d.f. = 122, $P < 0.001$). On the Main Stem, the smallest sized gravid turtle was 132 mm CL, and all size-class bins were represented from 135 to 165 mm CL (Fig. 2). For the South Fork, in the 1990s, one gravid turtle was 132 mm CL, and the next smallest gravid female over both decades was 149 mm CL, with no individuals detected between those sizes (Fig. 2). Given that the single 132 mm CL South Fork turtle was substantially smaller than the next smallest gravid female at 149 mm CL (Fig. 2), in further analyses we consider the minimum size at reproductive maturity to be 149 mm CL for the South Fork. We compare these values to those from other studies of western pond turtles (Table 3).

Environmental data

The mean number of growing degree-days per year (GDD year⁻¹) based on four stream gages were 1649.2 for South Fork (data from 2001 to 2009), 404.9 for Douglas City (data from 2000 to 2008), 272.1 for Limekiln

Table 3 Summary of minimum and average carapace lengths (CL) in mm for gravid female western pond turtles (*Actinemys marmorata*)

Minimum CL	Average CL	Location	Source
139	144.8*	Santa Barbara County, CA	Germano & Rathbun (2008)
144	154.3*	Fresno County, CA	Germano (2010)
144	158.3*	Fresno County, CA	Germano (2010)
140	151.6	San Luis Obispo Co., CA	Scott <i>et al.</i> (2008)
133	144	Mojave River, CA	Lovich & Meyer (2002)
132	154.9	Trinity River, CA	Current study
149 [†]	169.7	South Fork Trinity River, CA	Current study

*Reported value represents the average carapace length of all adult females from the study because the mean of all gravid females was not reported; however, >50% of females observed were gravid.

[†]Omits one record from 1994 of a 132 mm CL gravid turtle as this value did not appear to be representative of gravid females from this river (Fig. 2).

(data from 2001 to 2008) and 794.4 for North Fork (data from 2000 to 2004; Fig. 3). We considered these values to be representative of temperatures experienced by turtles as follows: South Fork data represent the South Fork data set, Douglas City data represent the Main Stem-1 data set, Limekiln data represent the Main Stem-2 data set, and North Fork data represent the Main Stem-3 data set. Daily mean values for GDD were used to convert turtle annual ages to GDD ages.

We found significant negative relationships between flow (log transformed m³ year⁻¹) at Lewiston, representative of releases from the dam, and annual GDD (GDD year⁻¹) at the Limekiln and Douglas City gages (Fig. 4a). At North Fork, no significant relationship between GDD and Lewiston flows was detected (Fig. 4a). Flows from the Lewiston Dam into the Main Stem have increased since the dam was completed, while South Fork flows have not shown a trend over a similar time period (Fig. 4b). Pre-dam Main Stem flows were similar to South Fork flows (Fig. 4b). Assuming the relationship detected between flow rates at Lewiston and annual GDD at Douglas City remained relatively constant, the annual GDD experienced by Main Stem-1 turtles has likely decreased since the completion of the dams (Fig. 4b).

Growth models

Two of the eight models with the smallest deviance information criterion (DIC) values had similar values

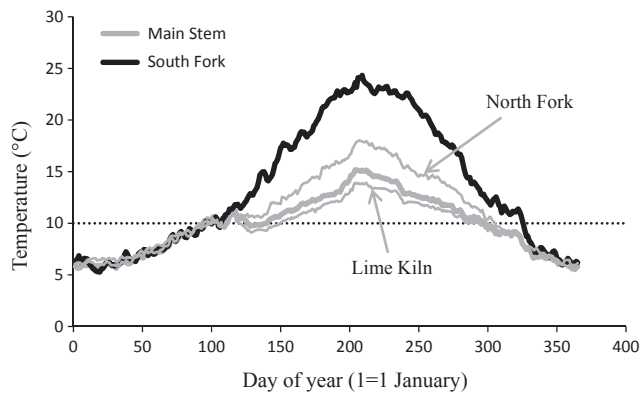


Fig. 3 Mean daily temperatures at four stream gages within the Trinity River system, Trinity County, California U.S.A. Black line is the South Fork gage, and thick grey line is the Douglas City gage, representing the locations of the majority of turtle captures. The Limekiln and North Fork gages, both of which are located on the main stem of the Trinity River near those locations, are indicated by the thin grey lines. For this analysis, we selected a threshold temperature of 10 °C, indicated by the horizontal broken line, with the assumption that no growth occurs below this temperature (see Fig. 2 for gage locations). Lewiston Dam is approximately 22 km upstream of Limekiln, 31 km upstream of Douglas City, and 62 km upstream of North Fork. Time frames for temperature data used from the four stream gages were as follows: Limekiln 2001–2008, Douglas City 2000–2008, North Fork 2000–2004 and South Fork 2006–2008.

($\Delta\text{DIC} = 1.2$), suggesting equal support for both models; thus, we carried our analysis forward using both models (Table 4). Both models include population-specific growth coefficient that describes the rate at which asymptotic length is reached (k) and the theoretical age at size 0 (t_0); however, there was relatively equal support for considering asymptotic length (L_∞) as either population-specific (Model 1) or common to both data sets (Model 2). The probabilities of the observed data occurring within the simulated data (P_{95}) were within acceptable ranges for all models, and the highest values were consistent with the models having the lowest DIC (Table 4). The mean parameter estimates were relatively consistent among all models (Table 5).

The lack of support for the reduced model that assumed the growth model parameters were the same for both populations indicated a distinction in size-at-age between South Fork and Main Stem-1, with the South Fork values being consistently higher than the Main Stem-1 values with very little overlap in size-at-age (Fig. 5a). When annual age was converted to GDD age, these distinctions diminished (Fig. 5b). Main Stem-1 turtles have slightly higher overall GDD growth rates than South Fork turtles, although there is a great deal of

more overlap in size at GDD age between the two data sets compared to size at annual age (Fig. 5a,b).

Age at reproductive maturity

We used the growth models to estimate expected annual and GDD ages for the minimum sizes of mature females from both populations (Table 6). We estimated annual and GDD ages for both 132 mm CL (Main Stem minimum) and 149 mm CL (South Fork minimum) for both populations to address the implications of delaying reproduction to larger sizes. For Main Stem females, delaying reproduction to 149 mm CL implies an 8- to 12-year delay in time to reproductive maturity, compared to only a 3-year delay for South Fork females (Table 6).

Juvenile growth rates

We estimated juvenile annual and GDD growth rates for all four data sets using least-squares linear regression. All regressions were significant with $P < 0.001$. The estimated annual growth rates were 14.0 mm year⁻¹ [95% confidence interval (CI) of 12.7–15.3] for South Fork, 6.3 mm year⁻¹ (95% CI = 5.0–7.5) for Main Stem-1, 6.5 mm year⁻¹ (95% CI = 2.5–10.5) for Main Stem-2 and 9.8 mm year⁻¹ (95% CI = 6.4–13.1) for Main Stem-3. There was a significant effect of location on growth rates (ANCOVA; $P < 0.001$), and *post hoc* test indicated that South Fork growth rates were higher than all Main Stem growth rates. Main Stem-2 growth rates were lower than Main Stem-3 growth rates. Main Stem-1 growth rates were not significantly different from either Main Stem-2 or Main Stem-3 growth rates.

Estimated GDD growth rates were 0.0085 mm GDD⁻¹ (95% CI = 0.0077–0.0093) for South Fork, 0.016 mm GDD⁻¹ (95% CI = 0.012–0.019) for Main Stem-1, 0.022 mm GDD⁻¹ (95% CI = 0.0088–0.036) for Main Stem-2 and 0.013 mm GDD⁻¹ (95% CI = 0.0082–0.017) for Main Stem-3. Again, we found a significant effect of location on GDD growth rates (ANCOVA; $P < 0.001$), and the *post hoc* tests indicated similar differences between the locations as was detected with annual growth rates, but with reversed directions. The South Fork GDD growth rates were lower than Main Stem GDD growth rates, and Main Stem-2 GDD growth rates were higher than Main Stem-3 GDD growth rates.

The earliest cohort year for the Main Stem-1990 data was 1983, and the latest capture date was 1996; hence, we used Lewiston Dam discharges between 1983 and 1996 to estimate the mean GDD year⁻¹ experienced by

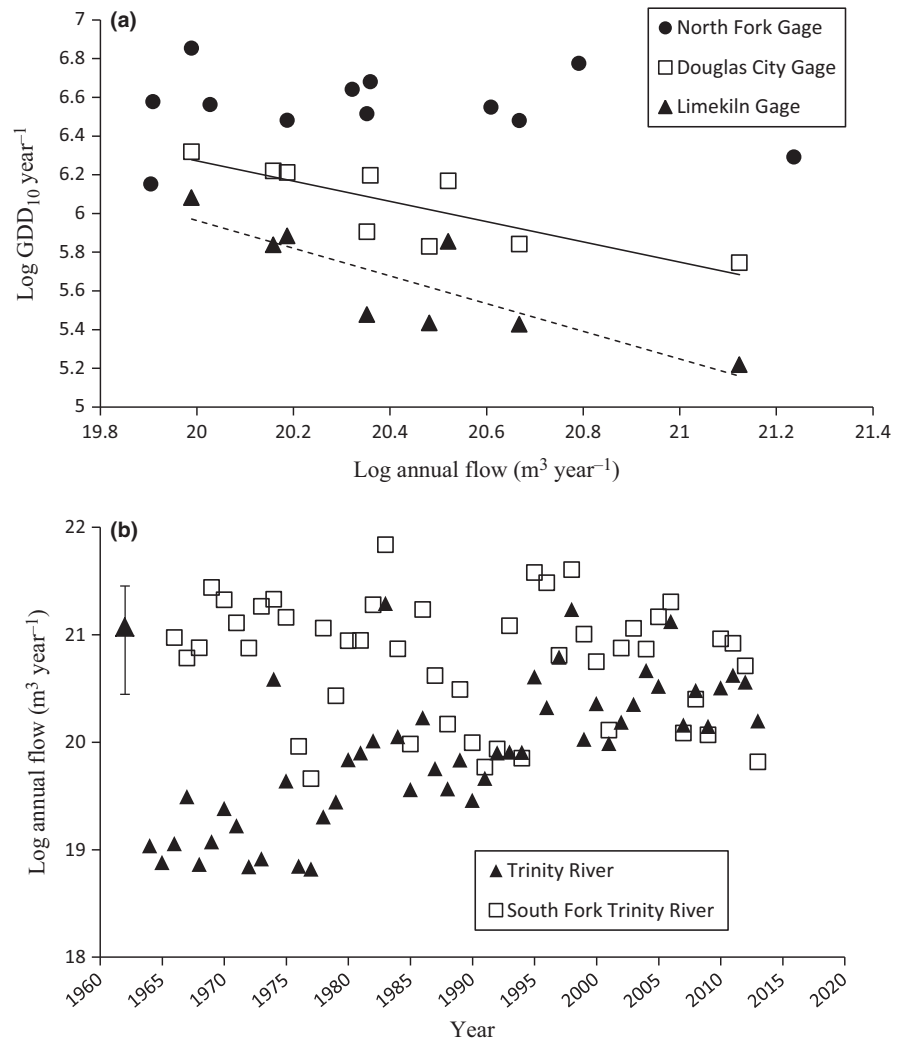


Fig. 4 (a) Relationship between annual growing degree-days above 10 °C (GDD) and annual discharge into the main stem of the Trinity River from the Lewiston Dam. Time frame for data used to estimate GDD year⁻¹ for each gage were as follows: Limekiln, 2001 to 2008; Douglas City, 2000 to 2008; and North Fork, 1993 to 2004. Lines are least-square linear regressions, dashed line is for the Limekiln gage data ($R^2 = 0.71$, $P > 0.05$), and solid line is for the Douglas City gauge data ($R^2 = 0.66$, $P > 0.05$). No significant relationship was found for the North Fork gage ($P = 0.74$). (b) For historical perspective, the annual discharge from the Lewiston Dam into the main stem of the Trinity River from 1964 to 2013, compared to the annual flows at the Hyampom gage on the South Fork Trinity River. The large solid triangle represents the mean flow of the Trinity River prior to the dam (1912 to 1962).

those turtles. Mean log discharge for those years was $20.14 (\pm 19.77) \text{ m}^3 \text{ year}^{-1}$. Using the mean relationship found in Fig. 4a for the Douglas City gage, this would represent an average of 492 GDD year⁻¹. Using the relationship between GDD growth rates and GDD year⁻¹ (Fig. 6), we would anticipate annual growth rates of 7.7 mm year^{-1} (95% CI 6.1 to 9.2). Our estimate of annual growth rate for the Main Stem-1990 juvenile data was 7.6 mm year^{-1} (95% CI 5.9 to 9.2; $P < 0.001$).

Juvenile growth rates and age at reproductive maturity

The observed slope between annual growth rate and GDD year⁻¹ was positive. However, it was less steep than the slope that described the relationship assuming equivalent GDD growth rates among the river segments (Fig. 6a). We found that GDD year⁻¹ explained 97% of the variation in mean juvenile annual growth rates between the four river segments. Conversely, we found

a significant negative relationship between GDD growth rates and log(GDD year⁻¹), in contrast to the lack of a relationship predicted from an assumption of equivalent GDD growth rates among the habitats (Fig. 6b).

We found a negative relationship for annual age at reproductive maturity between the populations inhabiting colder water (Main Stem) compared to warmer water (South Fork), assuming sizes at reproductive maturity of 132 mm CL and 149 mm CL, respectively (Fig. 6c). When we considered GDD age, the slope of the reaction norm switched; the Main Stem population reached reproductive maturity earlier than the South Fork population (Fig. 6d). While we consider 149 mm CL to be representative of the minimum size at reproductive maturity for South Fork females, there was one 132 mm CL gravid female (Fig. 2). However, the relationships observed in Fig. 6c,d would be the same if the size at reproductive maturity for South Fork females was 132 mm CL (Table 6).

Table 4 Comparison of fits for the eight models of western pond turtle (*Actinemys marmorata*) growth for the South Fork (subscript S) Trinity River and the main stem (subscript M) of the Trinity River, Trinity County, California, U.S.A. Parameters represent asymptotic length (L_{∞}), rate at which L_{∞} is reached (k), and theoretical age at size zero (t_0). Bolded values for the deviance information criterion (DIC) and Bayesian P value based on posterior simulations (P_{95}) indicate the best-fitting models for each assessment tool. pD is the effective number of parameters for each model

Parameters used in models	DIC	pD	P_{95}
Reduced model: $L_{\infty} k t_0$	5432.2	3.3	0.942
$L_{\infty} k_S k_M t_0$	4730.4	5.0	0.945
$L_{\infty} k t_{0,S} t_{0,M}$	5088.4	4.8	0.928
$L_{\infty,S} L_{\infty,M} k t_0$	4753.2	5.0	0.940
$L_{\infty} k_S k_M, t_{0,S} t_{0,M}$	4671.7	5.9	0.949
$L_{\infty,S} L_{\infty,M} k_S k_M t_0$	4694.5	5.9	0.940
$L_{\infty,S} L_{\infty,M} k t_{0,S} t_{0,M}$	4745.6	6.0	0.940
Full model: $L_{\infty,S} L_{\infty,M} k_S k_M, t_{0,S} t_{0,M}$	4670.5	6.3	0.948

Discussion

Given the differences in water temperatures, it is not surprising that we found substantial differences in growth rates, and age at reproductive maturity between South Fork and Main Stem populations. That the direction of the relationship between growth rate and water temperature reverses when annual growth rates are contrasted with growing degree day (GDD) growth rates was, however, an intriguing result. Considering annual growth rates (i.e. mm year⁻¹), Main Stem-1 juvenile turtles grew at about half the rate of South Fork turtles, and South Fork turtles reached equivalent adult sizes in a third of the time compared to Main Stem turtles. However, growth rates estimated without a reference to the thermal regime experienced by the individual can be misleading (Neuheimer & Taggart, 2007; Jessop, 2010). Accordingly, when growth was normalised for the thermal opportunity for growth (i.e. GDD growth rates; mm•GDD⁻¹), Main Stem-1 and Main Stem-2 turtles grew at nearly twice the rate of South Fork turtles (Neuheimer & Taggart, 2007). In addition, Main Stem-1 females reached reproductive maturity at 132 mm CL in 50% fewer GDD than South Fork turtles required to reach 149 mm carapace length (CL).

There could be other differences between the two rivers, in addition to water temperature, that influence the higher Main Stem GDD growth rates, such as food resources (Bury *et al.*, 2010), density (Neuheimer *et al.*, 2008) and basking habitat (Reese & Welsh, 1998b). However, the significant trend between GDD growth rates and temperatures along the Main Stem that we observed makes a compelling case for an environmentally induced

response to a thermally altered environment (Willemsen & Hailey, 2001), potentially mediated through basking behaviour (Reese & Welsh, 1998b). In addition, we were able to apply the relationships we found between total annual hypolimnetic discharge into the river, temperature and growth rates to accurately hindcast observed growth rates from a decade earlier. This result further supported our findings of a phenotypic response to decreased water temperature.

Phenotypic plasticity is generally defined as the ability of an organism to express a range of phenotypes in response to variation in the environment, and causal mechanisms include changes in biochemistry, physiology, morphology, behaviour or life history (Whitman & Agrawal, 2009). Aerial basking is a key thermoregulatory behaviour for aquatic emydids such as western pond turtles (Ben-Ezra *et al.*, 2008), and it is possible that this is the mechanism through which these turtles are manipulating their GDD growth rates. Reese & Welsh (1998b) found differences in habitat use by western pond turtles between the south and main forks of the Trinity River. While turtles selected habitats with deep, slow water containing submerged refugia in both rivers, those habitats in the South Fork were associated with dense canopy cover, warm water temperatures and limited basking structures. In contrast, the presence of basking structures appeared to be more associated with the presence of turtles on the Main Stem. It appears that South Fork turtles rely more on water basking for thermoregulation, while Main Stem turtles rely on aerial basking, potentially influencing the counter-gradient growth rates we observed. Detailed studies are needed to fully explore the relationship between basking behaviour, the resulting cumulative body temperatures and GDD growth rates.

Western pond turtles can be reliably aged from annual scute marks on their plastrons (Bury & Germano, 1998; Germano & Bury, 1998). A limitation of this method, however, is the inability to assign age to large and/or old individuals. The reduction in growth rates following reproductive maturation makes it difficult to differentiate annual scute growth marks, and the surface of the scutes tends to wear down, obliterating the earlier growth marks (Bury & Germano, 1998; Germano & Bury, 1998). For the Trinity River system, age could be assessed for individuals up to about 16 year on the Main Stem, and about 8 year for the South Fork due to rocky substrates that wear scute marks (Ashton *et al.*, 2015). Mark and recapture studies provide growth rate information that inherently contains information on growth-at-size and by extension size-at-age (Fabens, 1965). This

Table 5 Summary of growth model parameter estimates for western pond turtles (*Actinemys marmorata*) on the South Fork (subscript S) Trinity River and the main stem (subscript M) of the Trinity River, Trinity County, California, U.S.A. Parameter estimates, reported as mean, median (in italics) and 95% posterior intervals (in brackets) for the von Bertalanffy growth function for each of the eight models described in Table 3. Parameters represent asymptotic length (L_{∞}), rate at which L_{∞} is reached (k), and theoretical age at size zero (t_0). 'Specific' indicates that the model assumed the parameter values that were different for each river, while 'common' indicates an assumption that the parameters were the same for both rivers. Bolded rows indicate the models that provided the best fits to the data

Model	$L_{\infty,S}$	$L_{\infty,M}$	L_{∞}	k_S	k_M	k	$t_{0,S}$	$t_{0,M}$	t_0
L_{∞} = common	—	—	149.9	—	—	0.102	—	—	-5.27
k = common	—	—	149.5	—	—	0.102	—	—	-5.23
t_0 = common	—	—	[141.6,160.9]	—	—	[0.079,0.127]	—	—	[-6.69,-4.09]
L_{∞} = common	—	—	166.5	0.189	0.091	—	—	—	-1.70
k = specific	—	—	166.4	0.189	0.091	—	—	—	-1.69
t_0 = common	—	—	[162.4,170.8]	[0.173,0.205]	[0.085,0.097]	—	—	—	[-1.93,-1.48]
L_{∞} = common	—	—	170.1	—	—	0.098	-5.14	-1.22	—
k = common	—	—	169.9	—	—	0.098	-5.13	-1.21	—
t_0 = specific	—	—	[161.6,180.1]	—	—	[0.085,0.112]	[-5.79,-4.54]	[-1.74,-0.75]	—
L_{∞} = specific	181.2	127.6	—	—	—	0.158	—	—	-1.82
k = common	181.1	127.5	—	—	—	0.158	—	—	-1.81
t_0 = common	[176.0,186.7]	[124.3,131.1]	—	—	—	[0.145,0.171]	—	—	[-2.06,-1.59]
L_{∞} = common[†]	—	—	168.1	0.201	0.074	—	-1.38	-3.62	—
k = specific	—	—	168.0	0.201	0.074	—	-1.37	-3.61	—
t_0 = specific	—	—	[164.2,172.3]	[0.186,0.216]	[0.068,0.080]	—	[-1.57,-1.20]	[-4.31,-3.00]	—
L_{∞} = specific	170.7	142.9	—	0.186	0.123	—	—	—	-1.59
k = specific	170.6	142.7	—	0.186	0.123	—	—	—	-1.59
t_0 = common	[166.3,175.4]	[136.8,149.6]	—	[0.171,0.201]	[0.110,0.136]	—	—	—	[-1.81,-1.39]
L_{∞} = specific	179.0	129.6	—	—	—	0.159	-1.88	-1.35	—
k = common	178.9	129.6	—	—	—	0.159	-1.87	-1.34	—
t_0 = specific	[173.9,184.4]	[126.1,133.5]	—	—	—	[0.147,0.173]	[-2.12,-1.64]	[-1.71,-1.01]	—
L_{∞} = specific*	169.0	158.0	—	0.199	0.087	—	-1.39	-3.18	—
k = specific	168.9	157.5	—	0.198	0.086	—	-1.39	-3.16	—
t_0 = specific	[165.0,173.2]	[146.7,172.1]	—	[0.183,0.214]	[0.070,0.104]	—	[-1.59,-1.20]	[-4.04,-2.42]	—

*Model 1.

†Model 2.

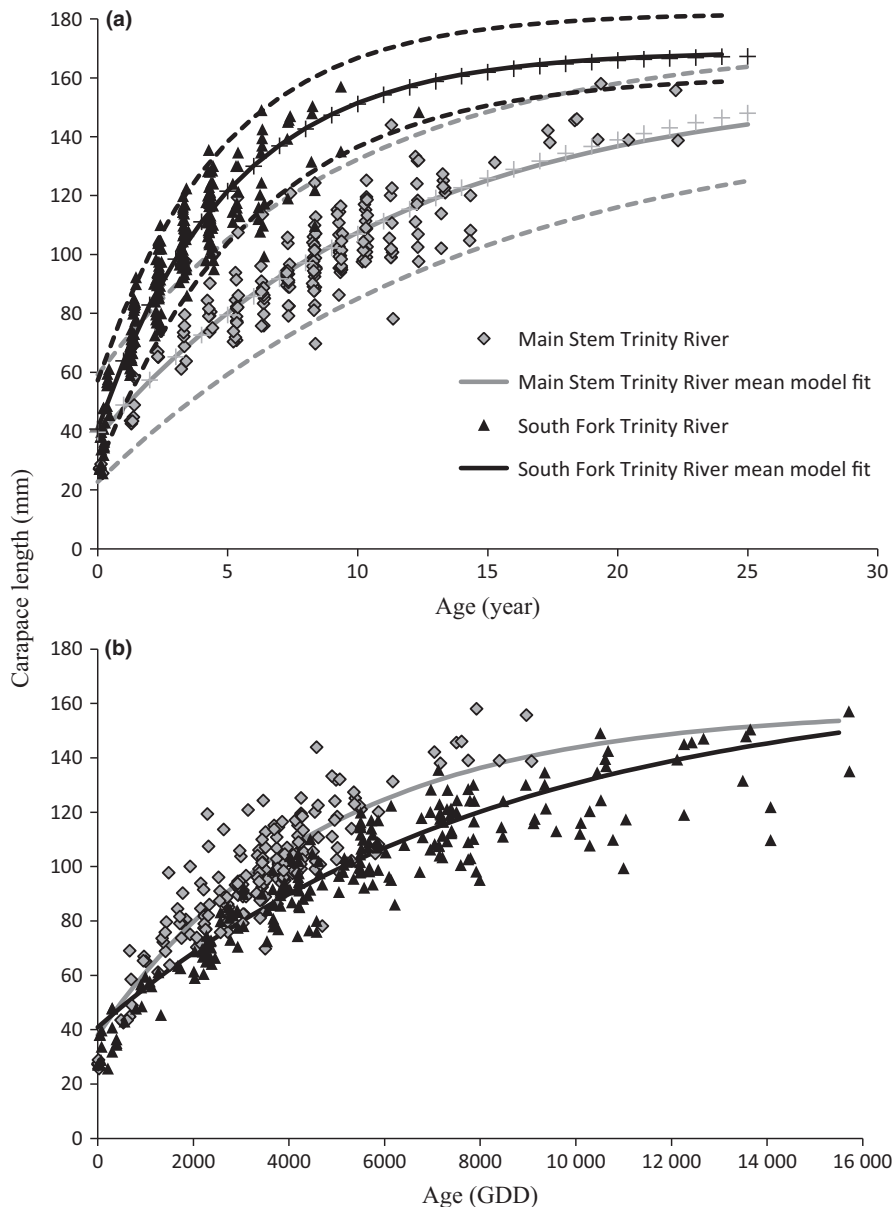


Fig. 5 Size-at-age for western pond turtles (*Actinemys marmorata*) in the Trinity River system; grey diamonds are from the main stem of the Trinity River, and black triangles are from the South Fork Trinity River (both a and b). (a) Solid lines represent the fit of Model 1 to the data using mean values for parameter estimates; grey line is for the main stem of the Trinity River, and the black line is the South Fork Trinity River. Broken lines show the range of variation expected (2.5 and 97.5 percentiles), and colours are consistent with solid lines. Plus symbols trace the fit of Model 2 to the data using mean values for parameter estimates with colours consistent with solid lines. (b) Age from the top graph was converted to growing degree-days using a threshold temperature of 10 °C (GDD) and mean numbers of GDD per year based on stream gage data. Solid lines represent the same mean model fit (Model 1) as in (a), converting the model parameters to units of GDD. Symbols and line colours are the same as in (a).

relationship has been used to develop somatic growth models using growth-at-size information only (e.g. Zhang, Lessard & Campbell, 2009; Eguchi *et al.*, 2012; Aven & Snover, 2013). Recently, Armstrong & Brooks (2013) presented a model that incorporates both size-at-age and growth-at-size information to estimate growth model parameters for snapping turtles. Adapting the models of Armstrong & Brooks (2013), we were able to leverage the use of both sources of data to enhance our understanding of size-at-age over the entire ontogeny of western pond turtles in the Main Stem and South Fork. Due to a lack of known-aged large turtles, other growth models for western pond turtles have estimated L_{∞} based on upper decile lengths of adult turtles, making

the values a constant in the models (Germano & Bury, 2009; Bury *et al.*, 2010; Germano, 2010). Within the von Bertalanffy growth function, the parameters for mean asymptotic length (L_{∞}) and intrinsic growth rate (k) are directly proportional (Snover, Watters & Mangel, 2005). Hence, making L_{∞} a constant in the model will influence the value of k , rather than allowing the data to inform the distribution of those parameters. With our approach, we were able to make inferences regarding these parameters based on the data, facilitating comparisons across populations.

Our growth model results gave relatively equal support to two of the growth models. Model 1 indicated that there were different mean population asymptotic

Table 6 Age-at-size for female western pond turtles (*Actinemys marmorata*) for the South Fork Trinity River (South Fork) and the main stem of the Trinity River (Main Stem), Trinity County, California, U.S.A. based on the von Bertalanffy growth function and using parameters for the best-fitting models. Model 1 assumed that the asymptotic length (L_{∞}), rate (k) and theoretical age at size zero (t_0) parameters were different for each river, while Model 2 assumed that L_{∞} was the same for both rivers, with k and t_0 values specific to each river. A dash indicates that the size was greater than the asymptotic length for that model, making it impossible to calculate an age. Numbers reported are based on mean parameter estimates, 95% prediction intervals for parameter estimates in brackets and estimated total growing degree-days $>10^{\circ}\text{C}$ needed to achieve size in italics

Size (mm CL)	Source	South Fork Model 1	South Fork Model 2	Main Stem-1 Model 1	Main Stem-1 Model 2
132	Smallest size of gravid females found on the MS in the 1990s	6.4 [4.4,9.2] 10 523	6.4 [4.3,9.5] 10 583	18.1 [10.2,31.6] 7339	17.5 [12.2,24.9] 7088
149	Smallest size of gravid females detected on the South Fork with the exception of one gravid female record from 1994 of 132 mm	9.3 [6.3,14.2] 15 394	9.4 [6.1,15.1] 15 576	29.9 [15.2, -] 12 119	25.7 [17.4,38.7] 10 411

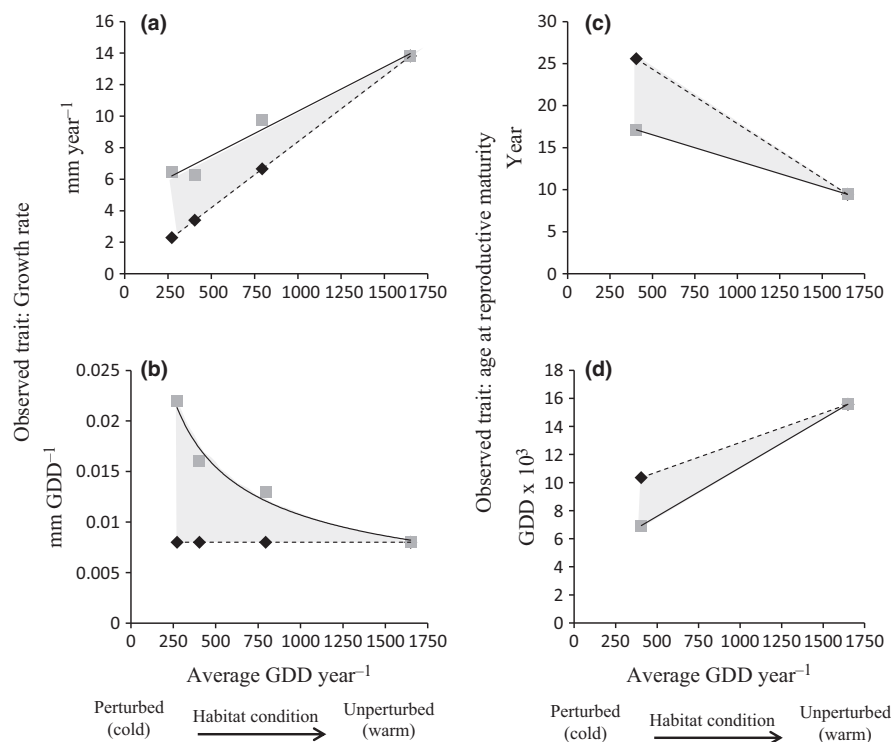


Fig. 6 Juvenile growth rates and age at reproductive maturity traits for western pond turtles (*Actinemys marmorata*) as functions of growing degree-days per year (GDD year⁻¹) using a threshold temperature of 10 °C. In all plots, dashed lines are the hypothesised phenotypes based on the assumption of no growth compensation (i.e. the same GDD growth rate at all temperatures), and black diamonds are the GDD year⁻¹ of the habitats studied; solid lines are the observed trends, solid grey squares are the mean observed data, and shaded areas highlight the magnitude of the difference between the hypothesised and observed trends. (a) Observed trend has a significant positive linear relationship ($r^2 = 0.97$; $P < 0.05$). (b) Observed trend has a significant negative power relationship with a scaling exponent of -0.53 ($r^2 = 0.98$; $P < 0.05$). (c and d) Age (year and GDD) for the cold habitat of the main stem of the Trinity River is based on a size at reproductive maturity of 132 mm CL; for the warm habitat of the South Fork Trinity River, the age values are based on 149 mm CL.

lengths (L_{∞}) and intrinsic growth rates (k), with higher values for both parameters for the South Fork. Model 2 suggested that mean population L_{∞} is the same for both populations and that there is a greater disparity in k values between the two rivers compared to Model 1. The

model parameters for the South Fork were nearly identical between the two best-fitting models. While the smaller size of adult gravid females found on the Main Stem suggests support for different values of L_{∞} between the rivers, it is also possible that adult Main Stem females

still have the capacity to achieve large sizes. However, under current water temperatures, they would not attain these sizes until ages approaching 40 year and, even at relatively high survival rates, few individuals are expected to reach this age. Alternatively, the high support for Model 2 could be due to the inclusion of size-at-age data based on initial captures in the 1990s in the Main Stem-1 data set. We found that growth rates were higher in the 1990s, likely due to lower flows from the dam resulting in higher water temperatures, and these size-at-ages could imply a higher mean L_{∞} than what the population is currently exhibiting (Ashton *et al.*, 2015). In a comparative analysis of both males and females between the South Fork and the Main Stem, Ashton *et al.* (2015) found that the proportion of adult-sized turtles >160 mm CL decreased from 14% in the 1990s to 7% in the 2000s on the Main Stem, while the South Fork showed no change between decades.

By converting the von Bertalanffy growth function parameters from year to GDD units, we were able to assess how growth and maturity compared between the populations based on this measure of physiological time. Neuheimer & Taggart (2007) assert that measures of the thermal opportunity for growth, such as GDD, have greater power to explain variability in size-at-age compared to calendar time. They demonstrate that GDD can explain >92% of the variation in length-at-day for fish populations under widely different conditions including marine and freshwater environments in temperate and tropical climates. Our results support this finding when comparing size-at-age between populations of an aquatic turtle that uses both aquatic habitats and aerial basking structures to thermoregulate. In spite of this thermoregulatory behaviour, the variability in size-at-age between South Fork and Main Stem-1 turtles was greatly reduced when physiological age, based on water temperature, was considered. For example, for calendar age, the difference between mean lengths at annual age of 5 year between the populations was 41.1 mm (80.5 mm CL for Main Stem-1 and 121.6 mm CL for South Fork). In contrast, at GDD age 2046 GDD, the difference between mean lengths was only 11.6 mm (80.5 mm CL for Main Stem-1 and 68.9 mm CL for South Fork). The GDD growth models also revealed that Main Stem-1 turtles grew at a significantly faster rate compared to South Fork turtles. This increase in growth, however, was not enough to fully compensate for the temperature differences between the two rivers. It is interesting to note that although the difference was not significant, Main Stem-2 turtles may be compensating enough to grow at least as fast if not faster than Main Stem-1 turtles. While

the average GDD year⁻¹ experienced by Main Stem-2 turtles was considerably lower than that of Main Stem-1 turtles, the annual growth rates were slightly higher. Overall, we found that annual growth rates increase at an average rate of 0.0056 mm year⁻¹ per GDD. The power relationship we detected between GDD growth rates and total GDD year⁻¹ suggests that, in the Trinity River system, western pond turtles are increasing their growth compensation in direct proportion with decreasing GDD year⁻¹ with a proportionality constant of 0.53.

Similar patterns of growth compensation have been observed in numerous other ectotherms, including fish (Chavarie *et al.*, 2010; Rypel, 2013; Sinnatamby *et al.*, 2015), amphibians (Berven, Gill & Smith-Gill, 1979) and invertebrates (Trussell, 2000; Heilmayer *et al.*, 2005). When the growth compensation is shown to be the result of genetic adaptation, the phenomenon is called counter-gradient variation (Conover & Present, 1990; Conover & Schultz, 1995; Conover, Duffy & Hice, 2009). Through common garden experiments, Conover & Present (1990) found that Atlantic silversides (*Menidia menida*) from high latitudes outperformed fish from low latitudes when reared in similar temperature conditions. They suggest that Atlantic silversides from higher latitudes are genetically adapted for rapid elevation of growth rates during shorter and cooler growing seasons, with one selection mechanism for this phenotype being size-dependent winter mortality. Western pond turtle populations in the Trinity River system are likely not completely isolated from each other, and the thermal regime of the Main Stem may be too recent for genetic adaptation to explain the counter-gradient pattern we observed. More likely, the pattern is explained by the capacity for phenotypic responses to environmental perturbations, potentially inherent in both populations, and possibly common to the species (Shine & Iverson, 1995).

While the proximate cause of the counter-gradient growth we found may be different from the genetic basis reported based on common garden experiments (Conover & Present, 1990; Rypel, 2012a), similar life-history trade-off questions remain. The rate at which animals should grow and the timing of reproductive maturity that together maximise fitness has received much attention (e.g. Stearns & Koella, 1986; Berrigan & Charnov, 1994; Shine & Iverson, 1995; Willemssen & Hailley, 2001; Day & Rowe, 2002). In general, there should be a strong impetus for rapid juvenile growth rates (Stearns, 1989) as this leads to decreased age at reproductive maturity, increasing the likelihood of surviving to reproduce. Counter-gradient growth suggests that some populations are growing at submaximal growth

rates. South Fork turtles may have the capacity to grow at a much faster annual rate; however, they have reduced intrinsic growth rates compared to the Main Stem-1 and Main Stem-2 locations. Similarly, if Main Stem-3 turtles grew at the same GDD growth rate as Main Stem-1 turtles, they would almost fully compensate for the temperature differences between Main Stem-3 and South Fork (12.7 compared to 13.8 mm year⁻¹). Negative trade-offs between rapid growth and physiological performance or life-history variables have been detected, potentially justifying reduced growth rates as trade-offs for the potential decrease in survival. For Atlantic silversides, Billerbeck, Lankford & Conover (2001) found a negative relationship between locomotory performance and intrinsic growth rates whereby the faster-growing northern population exhibited slower bursts and prolonged swimming speeds. Similarly, Lankford, Billerbeck & Conover (2001) found a relationship between intrinsic growth rates and vulnerability to predation, with higher predation rates on the faster-growing northern population in laboratory studies of Atlantic silversides. Hence, reduced GDD growth rates may convey a fitness benefits to western pond turtles in warmer environments.

Changes in size and age at reproductive maturity are a common phenotypic response to reduced growth opportunity for juveniles (Stearns & Koella, 1986). Delaying reproduction and initiating reproduction at a smaller size, which likely reduces individual fecundity, is a life-history adaptation than can minimise the loss of fitness conveyed by lower quality environments that decrease juvenile growth rates (Stearns & Koella, 1986). Counter-gradient growth offsets environmental gradients by minimising the variation in life-history traits such as age to reproductive maturity across those gradients (Conover & Schultz, 1995). At all of the possible sizes at reproductive maturity we assessed, Main Stem-1 females took approximately three times as long to achieve those sizes as South Fork females. The age at reproductive maturity for Main Stem females (18 year) is approximately twice as old as for South Fork females (9 year). Without counter-gradient growth, assuming the same GDD growth rate measured for the South Fork, Main Stem females would reach 132 mm CL in an average of 27 years. With counter-gradient growth, Main Stem females are able to achieve this size 9 year sooner, increasing the likelihood of surviving to reproductive maturity. If we reverse this and assume South Fork turtles have the capacity to grow at the same GDD growth rate as Main Stem-1 turtles, they would reach 132 mm CL between 4 and 5 year, and 149 mm CL between 6

and 7 year. Hence, there is only a 2- to 3-year delay in reproductive maturity if the observed South Fork turtle GDD growth rates are submaximal. This delay may trade-off with other benefits conferred from a reduction in intrinsic growth rates, as discussed above, including decreased predation mortality or enhanced locomotory performance (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001).

The minimum size at reproductive maturity for South Fork turtles, excluding the single turtle measured at 132 mm in the 1990s, is the largest reported in the literature (Lovich & Meyer, 2002; Germano & Rathbun, 2008; Scott *et al.*, 2008; Germano, 2010). Larger adult body size conveys a fitness advantage for female turtles in terms of larger clutch sizes, larger eggs or both (Congdon & Gibbons, 1983; Galbraith, Brooks & Obbard, 1989; Scott *et al.*, 2008; Germano, 2010). While growth in freshwater turtles is indeterminant, growth rates slow substantially after females become reproductive (Bury, 1979; Galbraith *et al.*, 1989); hence, delaying reproductive maturity to a larger size can increase lifetime reproductive output. With decreased opportunity for growth, turtles must trade-off the risk of not surviving to reproduce with the increase in fecundity brought by reproducing at a larger size (Willemsen & Hailey, 2001; Scott *et al.*, 2008; Germano, 2010). For Main Stem turtles, the difference between 132 mm CL and 149 mm CL is 8–10 years, imposing a substantial risk of not surviving to reproduce, compared to only a 3-year difference for South Fork. Based on the relationship between carapace length and clutch size for western pond turtles found by Germano (2010), this size difference can also mean an increase in clutch size from approximately four eggs at the smaller size to seven eggs at the larger size, a difference that could substantially increase lifetime reproductive output.

Reptiles in general and turtles specifically have plastic life histories that allow them to adapt to environmental changes (Shine & Iverson, 1995; Spencer & Janzen 2010). Based on our results, it is likely that juvenile growth rates of Main Stem western pond turtles have undergone a dramatic decline over the past 50 years although the impacts of this decline on their population dynamics is unclear. Changes in size and age at reproductive maturity are a common phenotypic response to reduced growth opportunity for juveniles (Stearns & Koella, 1986). Delaying reproduction and initiating reproduction at a smaller size, which likely reduces individual fecundity, is a life-history adaptation than can minimise the loss of fitness conveyed by lower quality habitats that decrease juvenile growth rates (Stearns & Koella, 1986).

We plan to address the issue of the viability by developing population models that combine the current temperature-driven growth models with an analysis of the mark-recapture data presented in this study to assess survival rates.

The reduced annual growth rates between rivers, although apparently mitigated by a GDD growth rate displaying a thermal counter gradient, suggests delayed reproductive maturity in females of at least 9 years for the Main Stem compared to the South Fork. To our knowledge, no other studies of turtle growth have applied GDD, nor has a counter-gradient growth pattern been documented for any turtle species. Our study highlights the applicability of GDD to understanding growth rates of aquatic turtles. It also highlights a mechanism for population adaptation to altered thermal regimes through increased intrinsic growth rates. Understanding the interplay of phenotypic responses to altered environments is critical for conservation and management. The results of this study add to our understanding of the capacity for phenotypic responses to altered environments in western pond turtles. The predictability of the response provides a management tool for understanding the impacts of dam-altered thermal regimes including the cumulative impacts of annual dam flow rates on population productivity.

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