Comparative Ecology of Western Pond Turtle (*Actinemys marmorata*) populations on the Free-flowing South Fork and Regulated Main Fork Trinity River: Demography, Size and Body Condition Comparisons, Thermal Ecology, and Spatial Dynamics

Final Report to the Trinity River Restoration Program

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INTRODUCTION

The western pond turtle (*Actinemys* = *Emys* [formerly *Clemmys*] *marmorata*) is widespread across the Pacific slope of North America, occurring in a wide variety of environments. They once were present almost everywhere aquatic habitats were available for at least a few months of the year, as long as appropriate terrestrial habitats for nesting, over-wintering, and aestivation were accessible. Formerly abundant, populations are now in decline throughout much of the historical range due primarily to habitat conversion for agriculture and urbanization, as well as from water diversions and competition from non-native species (Jennings and Hayes 1994; Bury and Germano 2008). The rivers of Northern California provide a stronghold for populations at the core of the species range, but even in remote areas, persistence can be threatened by resource uses such as water regulation and diversion. Here we compare ecological attributes, and by inference the relative fitness (the ability to produce subsequent generations), of turtle populations on the regulated (dammed) main stem fork of the Trinity River, Trinity County, California, with a population on the free-flowing south fork of this same river. We examined four areas of turtle ecology of particular interest because they can be adversely influenced by management actions: population demography, size and growth patterns, thermal ecology, and spatial dynamics.

Construction and operation of large dams worldwide have resulted in significant upstream and downstream changes to riverine environments (Poff and Zimmerman 2010); we focus here on downstream changes (Magilligan and Nislow 2005) due to the damming of the main stem Trinity River. The river was dammed in 1963 for water diversion and power generation, resulting in a suite of downstream hydrologic and structural changes in this system (Trush et al. 2000). Attenuation of floods necessary to maintain a dynamic alluvial system has allowed streamside encroachment of woody riparian vegetation leading to stable berm development and channelization of the river with a subsequent reduction of shallow edgewater habitats. Deviation from natural hydrograph patterns has disrupted life cycle functions of many riverine organisms. In addition, water is released from the cold lower strata near the bottom of the reservoir behind the dam (i.e., hypolimnetic release), manifesting in artificially low water temperatures in the main stem river below the dam during the summer.

Dam-induced alterations to the main stem Trinity River have led to dramatic declines in salmonids (USDI 2000; McBain and Trush 2000) and foothill yellow-legged frogs (*Rana boylii*; Lind et al. 1996). Western pond turtles are long-lived and possible impacts to their populations can take decades to become evident (see Rowe 2008). Three decades after dam construction a comparative demography study indicated impaired recruitment of young turtles into the main stem population compared to the free-flowing south fork (Reese and Welsh 1998a). We re-sampled these same populations to re-access these earlier findings and seek evidence of additional changes to turtles that may have occurred over the subsequent decade. By using the same capture techniques and study reaches (Reese and Welsh 1998a&b), we were able compare population parameters across the decade and between river forks to further investigate demographic differences between turtles living in the natural and controlled flow regimes (research topic 1). Differences in the sizes of adult turtles captured in our current efforts and those reported by Reese and Welsh (1998a) led us to suspect that impaired growth was occurring on the main stem (research topic 2). Ectotherms such as turtles are particularly sensitive to altered thermal regimes (Huey and Berrigan 2001), leading us to question whether differences observed in size and growth may be a response to the different thermal regimes of the two river forks. Consequently, we examined turtle thermal ecology by comparing basking behaviors and thermal profiles of individuals on the two forks (research topic 3). Finally, we compared locality data for turtles from the two forks, both between forks and with earlier localities from Reese and Welsh (1998a), to compare the spatial dynamics of the two populations at present, and when compared with localities from the 1990s (research topic 4).

RESEARCH TOPIC 1 - Comparative Demography of Western Pond Turtles on the Dammed and Free-flowing Forks of the Trinity River

Adult turtles can persist for decades at sites where juvenile recruitment has ceased, creating an often unnoticed, slowly-manifesting, extinction trajectory (e.g., Tilman et al. 1994). Consequently, demographic parameters like age structure are important to investigate because they can vary among populations under different environmental regimes (see Germano and Bury 2009). Detecting and tracking demographic parameters allows one to assess the relative status of target populations. For example, both fecundity and survivorship can vary by age (Ricklefs 1990; Charlesworth 1994). Detecting differences in key demographic parameters can

be critical for recognizing declining populations and helping to guide management decisions that promote species conservation. Based on previously reported differences in age structure between these turtle populations (Reese and Welsh 1998a), we hypothesized that we would find similar, or possibly more extreme, differences in age structure, and other demographic parameters, between the two river forks. In order to test these hypotheses we investigated and compared the following: age structure, survivorship, population estimates, sex ratios, in conjunction with estimating and correcting for capture probabilities.

RESEARCH TOPIC 2 - Comparison of Western Pond Turtle Size, Age, Growth, and Body Condition between Dammed and Free-flowing Forks of the Trinity River

Variations in growth rates, body sizes, and body condition can indicate important differences in the fulfillment of life history functions among animal populations, and these differences can have profound implications for fitness (Stearns 1992). Extrinsic factors that control body size can influence both individual and population fitness and ultimately population viability. Larger body size can infer advantages for turtles 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 rigid carapaces, having a larger body size can infer evolutionary advantages. In particular, a larger carapace can exceed gape limitations of many predators (e.g., mink, otter, raccoon, fox; all present in our study areas) (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).

Carapace length provides a relative index of turtle body size and it is not prone to the seasonal fluctuations that can occur with body mass. Maximum straight-line carapace length is commonly used to compare body size of turtles across systems (Lubcke and Wilson 2007; Germano and Bury 2009). Western pond turtles have demonstrated variability in body size in different environments (Lubcke and Wilson 2007; Bondi 2009; Germano and Bury 2009). Comparing age, size, growth and body condition of similar aged turtles allowed us to test the hypothesis of differences in these parameters between the two populations and by inference, differences in their physiologies and relative fitness.

Re-visiting these populations a decade after Reese and Welsh (1998a), we noted differences in mean carapace lengths of turtles on the main fork compared with those of the south fork, indicating possible impacts on fitness not detected in the earlier study. We compared carapace lengths between the two decades and the two forks to determine if there has been a significant reduction in the mean body size of turtles on the managed main fork.

RESEARCH TOPIC 3 - Basking Behavior and Thermoregulatory Profiles of Western Pond Turtles in Two Thermal Regimes

Bioenergetics plays a key role in the homeostasis of individual organisms (i.e., their ability to maintain internal physiological equilibrium). Ectotherms in particular rely on behavioral adaptations to thermoregulate (Huey and Kingsolver 1989). The primary behavior employed by freshwater turtles for this purpose is solar basking, using solar radiation to achieve and maintain optimal body temperatures. Thermal regulation is critical for the vital physiological functions of nutrient assimilation and growth. Growth rates affect size at sexual maturity, which in turn affect age- and size-specific reproductive investments and the size and number of offspring at birth. Female turtles that do not achieve full potential size can exhibit reduced reproductive potential, which ultimately can restrict the ability of a population to maintain itself through time. In effect, an altered thermal regime can negatively influence critical physiological processes required to maintain individual condition and the performance of key life history functions that contribute directly to population fitness and long-term viability.

Animals challenged by deviations from environmental conditions in which they have evolved can also incur chronic stresses that reduce their fitness. In ectotherms such stress can come from modified thermal regimes, both air temperatures and water temperatures (Stearns and Koella 1986). There are five developmental responses that ectotherms may exhibit when subjected to cold stress: 1) later maturity at a smaller size; 2) later maturity at a normal size; 3) later maturity at a larger size; 4) earlier maturity at a smaller size; or 5) they can mature at the same age but at a smaller size (Stearns and Koella 1986). Spotted turtles (*Clemmys guttata*) in the northern latitudinal limit of their range, attained a larger mean adult body size and reached sexual maturity at a later age, compared to southern populations (Litzgus and Brooks 1998); consistent with the 3rd response. In a study on egg-size relationships in the ectothermic Mediterranean gecko (*Hemidactylus turcicus*), a lizard with fixed clutch sizes, Selcer (1990)

found that clutch lipid mass was positively correlated with female snout-vent length (SVL) and body mass, and that egg mass was positively correlated to both hatchling mass and SVL. A study of three eastern species of turtles revealed that a structural constraint was placed on egg size by the size of the pelvic girdle and that the two smaller species were unable to maximize the size of their eggs (Congdon and Gibbons 1987). Change in body size due to cold stress may impact reproductive success by reducing clutch sizes (# of eggs per nesting season), reducing size of eggs, or both. The analysis of size at maturity of populations on the main fork and south fork in this report revealed that adult turtles are significantly larger at maturity on the south fork. The smaller sizes of female turtles on the main fork may be negatively influencing recruitment in this population. In this study we compared thermoregulatory behaviors and thermal profiles of turtles in each fork to test the hypotheses that important differences in basking behavior and thermal profiles exists between the two populations.

RESEARCH TOPIC 4 - Spatial Dynamics of Western Pond Turtles on Regulated and Free-flowing Forks of the Trinity River

Long-lived animals often rely on knowledge of local surroundings to locate important resources so site fidelity can influence individual fitness (Gibbons et al.1990; Clemmons and Buchholz 1997). Fidelity to specific sites for various life history functions has been reported for many Chelonians. Sea turtles, for example, return to their natal beaches for nesting (Ernst and Barbour 1989). In confined lentic waters, turtles often show allegiance to particular coves or areas of refuge (e.g., Andres and Chambers 2006). In rivers, turtles may exhibit fidelity to specific portions of channels (e.g., Reese 1996). The extent of movement can be an indication of habitat quality or stability (not necessarily synonymous). For example, home range size of gopher tortoises (*Gopherus polyphemus*) increased as forage quality or abundance decreased (Ashton and Ashton 2008). Dynamic riverine systems are predicted to promote site fidelity (Switzer 1993); however, the effect of flow management on fidelity is poorly understood and in need of further research.

Many studies of site fidelity, home range, and movement of turtles have employed radio-telemetry to elucidate short-term patterns, but telemetry studies are usually constrained by small sample sizes collected over short durations (e.g., Reese 1996; Arvisais et al. 2002; Litzgus and Mousseau 2004; Rowe et al. 2005; Innes et al. 2008). In contrast, longer-term

studies of spatial dynamics using mark-recapture methods generally had greater sample sizes, but fewer observations per individual (e.g., Pearse 1923; Cagle 1944; Andres and Chambers 2006). Here we used recent mark-recapture data in conjunction with data from Reese and Welsh (1998a) to compile a dataset spanning two decades.

Western pond turtles spend most of their active period in aquatic environments, relying on these areas for basking, foraging, refuge, and mating (Bury 1972; Reese 1996; Goodman and Stewart 2002). We reasoned that differences in thermal regimes between the two river forks would manifest in the two turtle populations showing different spatial dynamics. We tested this hypothesis by examining: (1) maximum distances moved between captures by sex; (2) whether turtles displayed similar amounts of movement in summer seasons on each fork; and (3) whether there were changes in movements by age or sex between study periods (i.e., between the two decades) and between the forks.

METHODS

Study Areas

We collected data from two major forks of the Trinity River, the free-flowing south fork (SFTR) and the dammed main stem fork (MSTR; Fig. 1). The main stem fork was dammed in 1963 for water diversion and power generation. Prior to damming, the main stem experienced dramatic impacts initially from large-scale placer mining, followed by hydraulic and later dredger mining. The south fork remains free-flowing, although it has an extensive timber harvest history. These two river forks have comparable drainage areas and, prior to the dam, had similar average annual flow (2460 km^2 and 2968 km^2, and 1.1 million and 1.2 million acre-feet, respectively [Reese and Welsh 1998a]). Both forks flow through mixed hardwood-conifer forests dominated by oak, madrone, grey pine, and ponderosa pine. Characteristics of the riparian areas differ between the two forks, in part due to geology, but primarily as a result of the dam. The main fork has dense shoreline vegetation, with large woody debris providing most of the available turtle basking substrates, whereas the south fork is bedrock-dominated with sparse shoreline vegetation and emergent rocks provide most basking sites (Reese and Welsh 1998b). While both forks experience winter rain and spring snow-melt peak flows, the main fork

is more snow-melt driven. Since damming, the stream flows of the main fork have been managed resulting in a suite of downstream environmental changes including increased channelization, lower water temperatures, less discharge and reduced extremes from flooding (Hampton 1995; Trush et al. 2000).

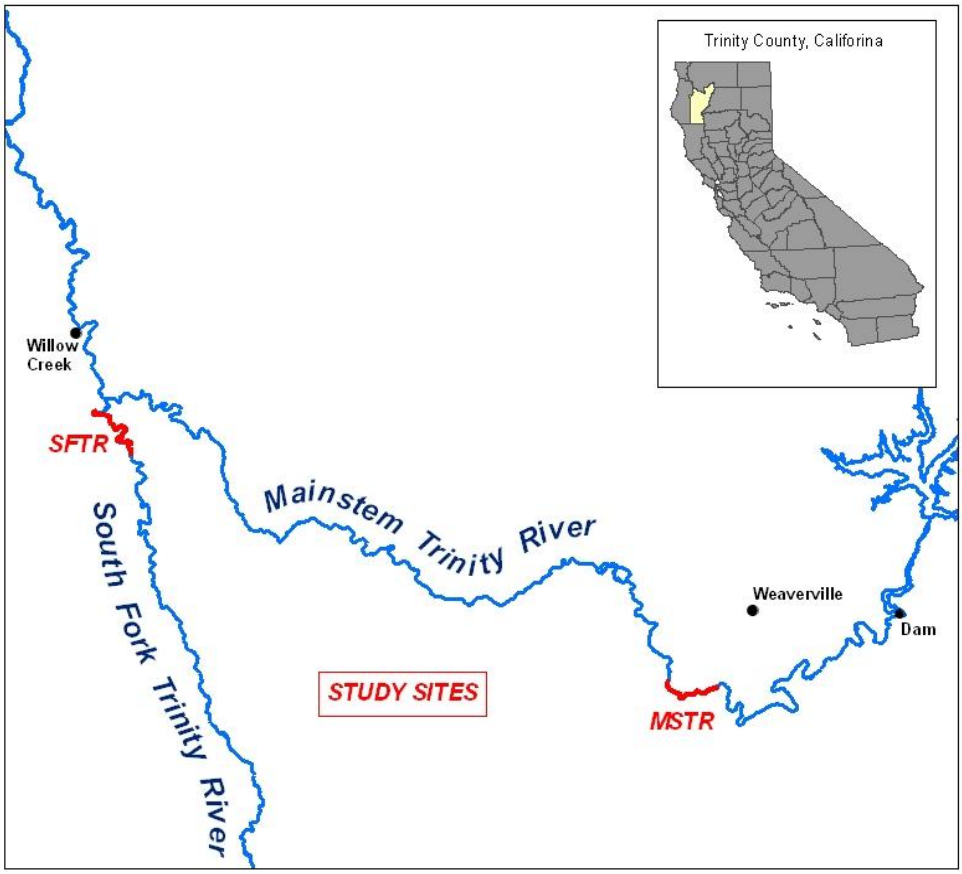


Figure 1. Map of study sites on two forks of the Trinity River, Trinity County, California. The main fork reach (MSTR) begins 38.2 km below the dam and continues downstream 5.6 km. The south fork reach (SFTR) begins 9 km above the confluence with the main fork and continues downstream 8.6 km.

Field Techniques

We conducted mark-recapture surveys to estimate demographic parameters of pond turtles during the summers of 2005, 2006, and 2007. Sampling methods and locations were based on surveys conducted from 1991-1994 (Reese and Welsh 1998a & b). Four censuses were conducted on each fork in 2005, five in 2006 and four in 2007 (Fig. 2). Surveys were typically

completed in three consecutive days on each fork, alternating weekly between forks during June, July, and August. Most surveys were conducted between 1100 and 1800 hr, but mid-summer lighting conditions permitted effective sampling to 2000 hr in some locations. We used inflatable kayaks to access study reaches. Two persons, one along each river bank, used masks, snorkel, and fins to swim and capture turtles. One diver searched along each bank and four meters out into the river channel, checking under boulders, logs, undercut banks, and root wads while also looking for basking turtles. Turtles were captured by hand. A third person followed in an inflatable kayak to receive and process captured turtles.

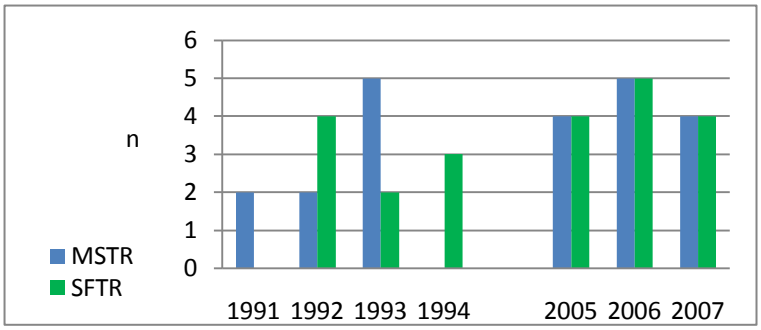


Figure 2. Number (n) of demographic sampling events per year for each river fork during both study periods. Years are grouped by study period (decades). There were nine sampling events per river fork in the 1990s and 13 sampling events in the 2000s.

Measurements and Photographs

For each capture we recorded time, location, general position and behavior (e.g., under a boulder, log/wood, in the open, basking), mass, age, sex, reproductive condition, and collected morphometric measurements (Table 1). We described and photographed injuries or health abnormalities. For most captures in the 2000s, we took digital photographs, including carapace, plastron, and a close-up of the posterior half of the plastron with a ruler for scale. Photographs were useful for confirming individual identity and verifying annuli counts used for age estimates. The photos were hyper-linked to individual records in the database and are archived at USFWS Arcata Office, USFS PSW Redwood Sciences Laboratory, and the Trinity River Restoration Program's Integrated Information Management System (IIMS).

Table 1. Morphometrics measured 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 which measurements were recorded in each study period (**Y**es / **N**o/ **I**ncomplete).

		Study Period	
Shell Measurement	**Caliper Position**	**2000s**	**1990s**
Carapace Length			
Maximum (CL)	greatest anterior to posterior span, parallel to midline; first or second marginal to twelfth marginal shield	Y	Y
Minimum (cl)	mid-line at posterior to cleft between nuchal and first marginal; either left or right	Y	I
Width (Cwd)	suture between second and third vertebral shield	Y	N
Plastron Length			
Maximum (PL)	greatest anterior to posterior span, parallel to midline; gular to anal shield; either left or right	Y	N
Minimum (pl)	plastron mid-line	Y	N
Width (Pwd)	suture between abdominal and femoral shields; at posterior edge of the bridge	Y	N
Shell / Dome Height	maximum dorso-ventral span	Y	N

We measured body mass using Pesola™ spring scales to the nearest 0.5 g for turtles > 100 g and to the nearest 1.0 g for turtles < 100 g. Sex and age class were determined by the presence or absence of sexually dimorphic characteristics, which develop in male turtles as they mature. Adult males have a concave plastron to facilitate mating, a whitish throat devoid of vermiculate patterning, a cloacal opening on the tail located beyond the distal margin of the posterior carapace, and compared to females they have a wider tail base to house the testes (Fig. 3; Bury and Germano 2008). Age class of females was determined by reproductive condition (determined by palpation) and size. Because of the lack of sexually dimorphic characteristics in younger individuals, external examination was not reliable and these turtles

were recorded as “unknown sex.” The exact age at maturation for these populations is unknown; size and/or age of maturation differs for the sexes and may differ between the two forks.

Figure 3. Female (left) and male (right) western pond turtles (*Actinemys marmorata*) from the south fork Trinity River.

Age Estimates

In both Reese and Welsh (1998a) and our study, the ages of individual turtles were estimated by counting annuli (growth rings) on the plastron (Gibbons 1990a; Stone and Babb 2005). While this method is not perfect (Wilson et al. 2003), it has been shown to provide a fairly 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; Germano and Bury 1998). Annuli do not provide a reliable age for older turtles because their annuli become worn over time and are difficult to accurately discern. The rockier substrate of the south fork causes turtles to develop a considerably worn plastron by the time they are about eight years of age, so we could not confidently count annuli on turtles >8 years old on the south fork. On the main fork where wood provides the primary basking substrate, annuli were often readable into the teens. When wear on annuli precluded accurate age estimates, turtles were classified by age group category: > 10 years of age (several annuli

could be counted but a few had been worn off); > 20 years of age (only a couple of annuli could be counted); and 99 + (when the entire plastron was smooth with no evidence of annuli). These groupings provided divisions within the adult age class for age-related analyses.

A summer growth season punctuated by a winter lag in growth is common in temperate freshwater turtles (e.g., Sexton 1959; Gibbons 1967). Close examination of photographs of plastron annuli for turtles less than 10 years old revealed a possible source of error due to mid-summer annuli deposition. Because our study coincided with the summer growth season, annuli count could change within sampling sessions. A turtle encountered early in the season may not yet show that season's annulus; however, within a few weeks the new annulus can become clearly visible. When the current season's annulus first becomes visible the turtle is approximately the same size as it was at the end of the previous growth season, potentially complicating size/age analyses. We re-evaluated the annuli counts obtained in the field for turtles less than 10 years old by scrutinizing the plastron photos under magnification. In nearly half of the cases (48%), age estimates were corrected based on photo annuli counts, recapture history, or a combination of the two. For comparative analyses of juveniles, we used corrected age estimates for turtles aged 2 to 8 years old.

Marking

Turtles were individually marked by filing notches on a unique set of marginal shields (Cagle 1939; Ferner 1979); this technique has previously been used with western pond turtles (Holland 1994). New captures in the 2000s were assigned marks 500 to 699 on the main fork and 775 to 1199 on the south fork. Reese and Welsh (1998a) used marks from 5000 to 6010; these differences eliminated potential for redundant marks between study periods and allowed us to easily recognize the decade of first capture for all recaptures. Some of the recaptures from Reese and Welsh (1998a) had chipped marginal scutes making some numbers difficult to decipher. In cases where data from the original study included capture location, sex, and maximum carapace length, we were able to narrow down the possible marks to a single option. In a few cases, original marks could not be deciphered and new marks were assigned.

Demographic Analysis (Research Topic 1)

Population Estimates Based on Mark-recapture Efforts

We estimated population sizes from mark-recapture data using Program MARK (White 2009). The analysis presented here compares only those data collected across the three years of the 2000s; in this report we did not compare our demographic data with the demographic data of Reese and Welsh (1998a) collected in the 1990s. As a point of clarification, we did compare data between the two decades in analyses that follow under other research topics. We treated each year of the 2000s data as primary samples with the within-year data treated as secondary samples. There were 13 secondary sample efforts on each fork over the three year period as follows: 2005 = four censuses, 2006 = five censuses and 2007 = four censuses (Fig. 2).

Three models were tested using the Robust Design; 'No Movement' Model, 'Random Movement' Model, and 'Markovian Movement' Model. For this, we introduced the gamma parameter (Υ) to account for the probability of an individual being "unavailable" for an encounter during one of the primary sampling periods. Furthermore, following Kendall *et al.* (1997) we extended the gamma parameter into gamma-prime (Υ') and gamma-double-prime (Υ''), where Υ' is the probability of being outside the boundaries of the study area and unavailable for capture during the first primary dive session and survives to the next primary dive session; and, Υ'' is the probability of being outside of the study area, and unavailable for capture during the first primary dive session given that the turtle *was* present during this session and survives to the next dive session. Each model was set based on gamma (Υ) parameters as follows: No Movement Model set $\Upsilon''_i = \Upsilon'_i = 0$; Random Movement Model set $\Upsilon''_i = \Upsilon'_i$; and Markovian Movement Model $p_i = c_i$. Estimates from each secondary sampling were averaged across the three primary sampling events to obtain a general population estimate for each river fork for the top model selected.

Population estimates were converted to turtle densities to make direct comparisons between the two populations. Population densities for each river were obtained by dividing the estimated population size by the area of the fork surveyed, which was obtained by multiplying

the reach length for each fork by its average width. The length of the main fork reach was 5.6 kilometers and the length of the south fork reach was 8.6 kilometers. Average widths were calculated using 10 evenly distributed width measurements along each reach. We also took a slightly more conservative approach to estimate the area of river surveyed based on our field protocol. This estimated survey area was obtained by multiplying the length of each reach by eight meters, four meters out for each bank surveyed, to omit the thalwag because turtles are poor swimmers and tend to avoid fast currents.

Adult Survival Estimates

Adult survival (Φ) for the four groups (main fork male/female, south fork male/female) was estimated using Program MARK (T_o test) by sex and river fork. We used seven candidate models. The first is a fully saturated global model to test for differences in survival (Φ) estimates between sex and river fork where both Φ and capture probability (p) are time dependent (Φ rs*t, p rs*t; where r = river fork, s = sex, and t = time dependence). Subsequent models included sex with time dependence, river with time dependence and survival with time dependence for both cases (i.e., capture probabilities either time-dependent or constant). Competing models were ranked by goodness-of-fit using corrected Akaike Information Criterion (AICc; Burnham and Anderson 1998). Over-dispersion was tested ($\hat{c}$ = 6.47 ± se for the top model): we adjusted accordingly to provide a quasi-likelihood estimator (QAICc); survival estimates were based on the top model.

Adult Capture Probabilities by River

Capture and recapture probabilities of western pond turtles were estimated using the Pradel model for data collected under the robust design. In all seven models, the probability of survival, Φ, was assumed to be constant across years and the seniority probability (the probability that an individual captured in one year was alive and in the population the previous year), ϒ, was allowed to vary across years. We modeled capture probability, p, and recapture probability, c, as a function of sex, site (main fork or south fork) and behavioral response. Under the behavioral response model, the capture and recapture probabilities were hypothesized to differ. The top model included p (behavior*site) and allowed for capture probabilities to vary by site and between capture and recapture probability. There was little evidence that p and c

varied between males and females. We used model-averaging to get estimates of p and c for each year, sex and fork.

Juvenile to Adult Ratios

To facilitate comparisons with the earlier research (Reese and Welsh 1998a), we defined juvenile turtles by a carapace length of < 125 mm and adults by a carapace length of ≥ 125 mm. Cross decade comparisons of juvenile: adult ratios were tested using chi-square analysis. We also calculated juvenile: adult ratios based on a size cut-off defined by the smallest mature male encountered during the demographic surveys to provide greater confidence that true adults were correctly represented in each population.

Comparison of Approaches for Defining Operational Sex Ratios

To thoroughly evaluate this important ratio we used four different size or age at maturity criteria: (1) included all initial captures, the first size cut-off for adults was a maximum carapace length of ≥ 125 mm (Reese and Welsh 1998a); (2) used secondary sexual characteristics to confirm the size of the smallest mature male (following Gibbons 1990b); (3) used the smallest known gravid females from each population as a cut-off (≥ 132 mm); and (4) we used ≥ 140 mm to define adult females (following Scott et al. 2008) as determined by radiographic evidence of gravidity.

Gravid Females

We used the earliest and latest dates of detection of gravid females to estimate the duration of the nesting season on the two forks. We reviewed earlier records of gravid females (Reese and Welsh 1998a) as well as those encountered during our demographic surveys in 2005-2007.

Size, Age, Growth, and Body Condition (Research Topic 2)

Size Comparisons

We compared the mean maximum carapace length (mm) by fork and decade with three analyses: 1) adult males and females > 125 mm using data from the first capture of each turtle; 2) largest (top 10% - upper decile) adult males and females for each fork and decade, using only the final capture in order to assess the maximum size obtained by each individual; and 3) turtles from two to eight years of known age regardless of sex to make direct comparison of size per

age using the last capture per year for each individual. To standardize search effort and growth period across factors we used only those animals captured during in June, July, and August (the core of the sampling period. Because size dimorphism is known for this species (Lubcke and Wilson 2007; Germano and Bury 2009) we included sex as a covariate for the first two analyses. The first analysis followed Reese and Welsh (1998b) by employing a size cut-off of 125 mm carapace length to define adults (n = 489). Turtles greater than eight years old with unknown sex were excluded (n = 28). Because we suspected the different thermal regimes of the two forks influenced the size structure of each population a strict size cutoff to define adults may not apply equally to both forks. Therefore the second and third analyses focused on the extremes of the available size/age classes, those well beyond the maturation period (i.e., the upper decile) or before expected maturation (2-8 year olds). By examining only the largest turtles, the second analysis eliminates potential bias due to errors in sex identification of smaller adults and differential growth rates or age of maturity. We selected the upper decile for each group by sex, fork, and decade, allowing us to compare adults of maximum size across these three factors and for direct comparison with Bury and Germano (2010). The third analysis allows for closer resolution of the early growth years and the period of recent river management following implementation of the new flow regime (USDI 2000). For the 2000s we verified age by annuli counts of plastron photographs. For the 1990s age was based on field observations. For comparisons we used ANOVA with fork and decade as factors (NCSS, Hintze 2004). Alpha was set at 0.1, a level appropriate for detecting ecological trends (Underwood 1997).

Growth Curves

We used morphometric and age data to examine and compare the patterns of growth for turtle populations on the two forks. To facilitate comparisons with other studies of western pond turtles, we ran two different model types commonly used in growth analysis: von Bertalanffy and Richard's growth models. We analyzed each population to determine model fit and to compare with recently published growth models (e.g., Bury and Germano 2009).

We ran separate growth analyses for specific subsets of the data to explore different aspects of growth. The first analysis included turtles < 10 years old in order to focus on the rapid growth of juveniles. The second analysis included animals that were encountered as

hatchlings early in the field season and individuals up to two years of age. This analysis was intended to determine the earliest and most rapid growth patterns and compare them between the two forks. We used a modified Julian Date based on a season of activity from April 1st through October 1st resulting in a 183 day potential growth timeline for each year. We defined turtles under the maximum carapace size of < 30mm as age 0, or "hatchlings". Turtles with a maximum carapace length of ≥ 30 mm were assigned age "1" and could occur in the same calendar year as hatchlings. We also included turtles classified as age "2" in order to compute "day" age; we took the number of days post April 1st that an individual was encountered and added this value to 183 days, which represented the previous growth season. We ran Richard's growth model on this collective data set of all encountered turtles aged two or less.

Body Condition

We compared body condition (body mass associated with energy reserves after correcting for body size) of adult animals (>125 mm carapace) between the two forks for each sex and decade. Data were analyzed separately by sex and decade due to sexual dimorphism and methodological differences in the collection of mass data between the two study periods. Body mass (log-transformed) was treated as the dependent variable and carapace length (log-transformed) was introduced as the adjustment covariate. Regressions were performed in NCSS (Hintze 2004).

Thermal Ecology (Research Topic 3)

We examined the thermal behavior of turtles captured on both forks during the spring and summer of 2005, 2006, and 2007 with data loggers placed on the external carapace to assess their thermal status. Grayson and Dorcas (2004) examined differences between external data logger readings and internal temperatures of turtles as measured by cloacal temperatures. They detected only a slight difference (mean = 0.26°C) between the two readings, suggesting that external data loggers accurately reflect the internal thermal response of turtle basking behavior (Grayson and Dorcas 2004). We fastened radio transmitters (PD-2 model, Holohil Systems Ltd.) and temperature loggers (Thermochron iButton, Alpha Mach Inc.) to the posterior carapace of turtles with putty epoxy (Dingleberries Surfboard Repair™ or Quiksteel). Data loggers were set to collect data every 60 or 120 minutes for 60 or 120 days. In addition, an array

of temperature loggers was placed in the water and on the bank to collect available ambient air and water temperatures for comparison to turtle-mounted temperature loggers.

We used water and air temperatures from the peak summer temperatures of July to compare with turtle temperature profiles (T_s) from the two river forks. When a T_s value was at least 1° C greater than these maximum water temperatures, the individual was assumed to have left the river channel to bask in direct sunlight or seek warmer aquatic thermal refugia. A T_s value lower than the maximum water temperature indicated that an individual was in the river. We calculated the amount of time each turtle had T_s values higher than the respective maximum water temperatures ("basking" time) and calculated the proportion of time spent basking by dividing "basking time" by the total time temperature loggers collected data within the month of July. We used T-tests and Yates Chi-square analyses to test for differences between the forks (NCSS; Hintze 2004).

Spatial Dynamics (Research Topic 4)

To examine spatial dynamics we used recapture data from 2005-2007 which we compared with data from 1991-1994 (Reese and Welsh 1998a). We searched only riverine habitats (i.e., no ponds or terrestrial habitats) with snorkel surveys between May and September of each year. Most surveys occurred in June, July, and August as our results were meant to characterize summer river channel use, and thus do not represent the entire potential annual home ranges of these animals. In the 1990s study the location of each capture was recorded as left or right bank and the distance in meters upstream or downstream to the nearest flagged station was visually estimated (Reese 1996). We digitized these locations using ArcGIS (9.2) based on mapped station positions. In the 2000s we used GPS coordinates or marks made on aerial photos to record and digitize capture locations. Topography of both river forks affected the accuracy of the locations obtained with a handheld GPS unit so GPS data were used only when mapped locations were not available. Turtle locations were projected onto NAD83, UTM zone 10N. A centerline covering each study reach was digitized for both forks using an NAIP aerial photo for Trinity County (USDA-FSA-APFO 2005). Using ArcGIS all turtle locations within 75 meters of the river centerline were "snapped" to associate them to the closest

centerline position. A distance of 75 meters retained turtles associated with the river habitats while omitting those associated with adjacent ponds or terrestrial habitats.

We performed spatial analyses using the linear referencing tools in Arc\Info™ (ESRI 2008). ESRI defines linear referencing as a method for storing geographic data by using a relative position along an already existing line feature and uniquely identifies positions along that line without explicit coordinates. In linear referencing locations are given an exact position along a defined line feature providing an intuitive way to associate multiple sets of attributes with portions of linear features. In this case, the linear feature was the river fork, and the location data were turtle captures along each fork. Linear referencing allowed us to associate both point location and movements for individual turtles.

We first determined whether differences in location recording protocols (between the 1990s and 2000s studies) had an impact on the observed positions of recaptured individuals. We detected no significant differences, so further analyses included both datasets. We used all turtles with at least two captures, with the greatest upstream and downstream locations used to determine the greatest distance moved by each individual. When an individual's sex could not be determined based on secondary sexual characteristics the animal was classified as unknown. In cases where turtles changed from unknown to male or female, they were assigned the sex of the most recent capture. The 21 cases where the recorded sex was switched between captures were not included in the analysis. Data were tested for normality and log-transformed when necessary. We used GLM ANOVA to examine differences in mean movement between forks, decades, and sex (SAS 2008).

We used a frequency distribution to describe total movement patterns for males, females, and unknowns. We assessed site fidelity by comparing between-year captures. A capture location was represented by either a point or a segment (line), depending on whether a turtle was captured once, twice, or more frequently in a given year. Based on literature suggesting aquatic home ranges of > 500 m of river channel (Holland 1994; Goodman and Rathbun 2000), we used a 250 m distance in either direction to represent movements away from an individual's primary aquatic activity area. Turtles recaptured within 250 m of a previous capture were designated as "sedentary" for that period; conversely, recaptures greater than 250 m from a

previous location were designated “nomadic.” All possible year combinations were compared to determine if individuals were “sedentary”, “nomadic”, or “not applicable” (i.e., individuals not captured in one of both years compared). The ratio of sedentary to nomadic designations provided individual indices of site fidelity.

RESULTS

Comparative Demography (Research Topic 1)

We captured 232 different turtles and had 223 recaptures, resulting in 455 total capture events on the main fork. On the south fork we captured 336 different turtles with 302 recaptures, resulting in 638 total capture events. We encountered three dead turtles over the three seasons, two main fork adult males and one south fork adult female. The south fork female had eggs and was evidently predated during a nesting foray; she was found about 20 meters upland from the river. The causes of death for the males are unknown. Dead turtles were recorded as a negative one in the encounter-history files (Cooch and White 2007).

Population Estimates Based on Mark-recapture Efforts

Population estimates for each fork based on program MARK are presented in Table 2. The top model on the main fork where we surveyed 12.35 ha yielded a population estimate of 220 turtles, resulting in 18 turtles/ha. The top model for the south fork where we surveyed 27.43 ha estimated 350 turtles, resulting in 13 turtles/ha (Table 2).

Adult Survival Estimates

A total of 350 individual encounter histories were recorded for adult turtles in the 2000s. The main fork had 57 adult females and 69 males, the south fork had 140 adult females and 84 males. The top model based on QAICc did not differ in survival estimates by fork or sex, however, survival varied over time when probabilities of encounters were held constant (Table 3). Survival estimates were 0.956 (SE = 0.053) for main stem adult males, 0.964 (SE = 0.071) for main stem adult females, 0.968 (SE=0.032) for south fork adult males, and 0.973 (SE = 0.092) for south fork adult females. The top model performed 3998 times (0.99973/0.00025) better than the next highest ranking model (Table 3).

Table 2. Population estimates for main stem (MSTR) and south fork (SFTR) by group and session (means in bold).

Population Estimate Model	Group	Session	Pop Est	Std Err	Lower CI	Upper CI
No movement model	MSTR	1	148	0.0007	148	148
	MSTR	2	228.55	26.82	186.19	293.27
	MSTR	3	283.67	33.8	228.37	362.59
		Mean	**220.07**	**20.21**	**187.52**	**267.95**
	SFTR	1	352.18	28.93	290.76	446.19
	SFTR	2	318.71	32.09	267.6	395.53
	SFTR	3	378.72	35.01	320.48	459.2
		Mean	**349.87**	**32.01**	**292.95**	**433.64**
Random movement model	MSTR	1	148	0.001	148	148
	MSTR	2	228.55	26.82	186.19	293.27
	MSTR	3	283.67	33.8	228.37	362.59
		Mean	**220.07**	**20.21**	**187.52**	**267.95**
	SFTR	1	352.18	38.93	290.76	446.19
	SFTR	2	289.7	38.39	234.26	390.16
	SFTR	3	384.42	36.55	323.79	468.65
		Mean	**342.10**	**37.96**	**282.94**	**435.00**
Markovian movement model	MSTR	1	148	0.001	148	148
	MSTR	2	228.55	26.82	186.19	293.27
	MSTR	3	283.66	33.8	228.37	446.19
		Mean	**220.07**	**20.21**	**187.52**	**295.82**
	SFTR	1	352.18	38.93	290.76	446.19
	SFTR	2	289.69	38.39	234.26	390.14
	SFTR	3	384.42	36.55	323.78	468.64
		Mean	**342.10**	**37.96**	**282.93**	**434.99**

Table 3. Comparison of western pond turtle (*Actinemys marmorata*) adult survival models. Φ = survival, p = capture probability, r = river fork, s = sex, t = time dependence, and (.) = constant.

Model	QAICc	Delta QAICc	AICc Weights	Number of Parameters
{ Φ (t) p (.)}	389.022	0.0	0.99973	13
{ Φ (t) p (t)}	405.640	16.618	0.00025	23
{ Φ (r*t) p (.)}	411.335	22.314	0.00001	25
{ Φ (s*t) p (.)}	413.436	24.415	0	25
{ Φ (r*t) p (t)}	428.021	38.999	0	35
{ Φ (s*t) p (t)}	430.680	41.658	0	35
{ Φ (r+s*t) p (t)}	480.010	90.989	0	59
{full (Φ (r+s*t) p (r+s*t))}	555.971	166.950	0	92

Adult Capture Probabilities by River Fork

Capture (p) and recapture probabilities (c) are reported in Table 4. These results indicate that initial capture probabilities were much greater than the recapture probabilities.

Table 4. Capture probabilities (p) and recapture probabilities (c) (with standard error in parentheses) for Western Pond Turtles (*Actinemys marmorata*) for male and females from 2005 to 2007 on the main stem (MS) and south fork (SF) Trinity River.

Primary Period	Females, MS	Males, MS	Females, SF	Males, SF
p, 2005	0.555 (0.054)	0.555 (0.054)	0.264 (0.036)	0.264 (0.036)
p, 2006	0.213 (0.032)	0.213 (0.032)	0.190 (0.023)	0.190 (0.023)
p, 2007	0.224 (0.050)	0.224 (0.050)	0.277 (0.041)	0.277 (0.041)
c, 2005	0.167 (0.025)	0.167 (0.025)	0.0143 (0.022)	0.0143 (0.022)
c, 2006	0.159 (0.028)	0.159 (0.028)	0.078 (0.014)	0.078 (0.014)
c, 2007	0.125 (0.038)	0.125 (0.038)	0.184 (0.031)	0.184 (0.031)

Operational Sex Ratios

Operational sex ratios varied slightly with differences in size cut-off criteria but generally were consistent by fork (Table 5). In all cases the south fork sex ratio was female-biased; on the main fork there was evidence of female bias only in the analysis of first time captures (Table 5).

Table 5. Operational sex ratios for initial captures on the main fork (MS) and south fork (SF) using different size criteria. Operational sex ratios are reported as males (M) to females (F), n (M) divided by n (F). Values less than 1.0 indicate a female-biased sex ratio; the lower the number, the more female-biased. Chi-square (X^2) statistic was used to test for significant deviation from an expected 1:1 ratio.

Differential size cut-offs	River	n (M)	n (F)	M:F	P
all first time captures[†]	MS	52	77	0.6753	0.0277*
	SF	79	138	0.5724	0.0000*
smallest male per river[‡]	MS	52	69	0.7536	0.1222
	SF	79	138	0.5724	0.0000*
carapace length > 126mm[+]	MS	41	55	0.7454	0.153
	SF	77	137	0.562	0.0000*
smallest gravid female (132mm)[‡]	MS	38	49	0.7755	0.2382
	SF	76	136	0.5588	0.0000*
size cut off of females at 140mm[◊]	MS	34	39	0.8717	0.5584
	SF	74	128	0.5781	0.0001*

* Significant difference; [†] all first time captures with recorded sex; [‡] criteria follows in subsequent analysis (Gibbons 1990b); [+] (Reese and Welsh 1998); [◊] (Scott *et* al. 2008).

Gravid Females

Between 1991 and 2007, 34 gravid females were found on the main fork and 81 on the south fork (Table 6). Marked differences appeared in the timing of egg deposition over this time period on the main fork with only two gravid females found in the 2000s (Fig. 4).

Table 6. The number of gravid female turtles, range of capture dates, sizes from all surveys (1991 - 2007) on the main fork (MS) and south fork (SF), and the number of gravid females captured just during the 2005-2007 surveys.

	MS	SF
N	34	81
Range of Dates	24May - 18July	21May - 28July
Average Maximum Carapace (mm)	148.22	169.77
Range of Maximum Carapace (mm)	132-173	132-186
Number Detected in 2005-2007 Surveys	2	46

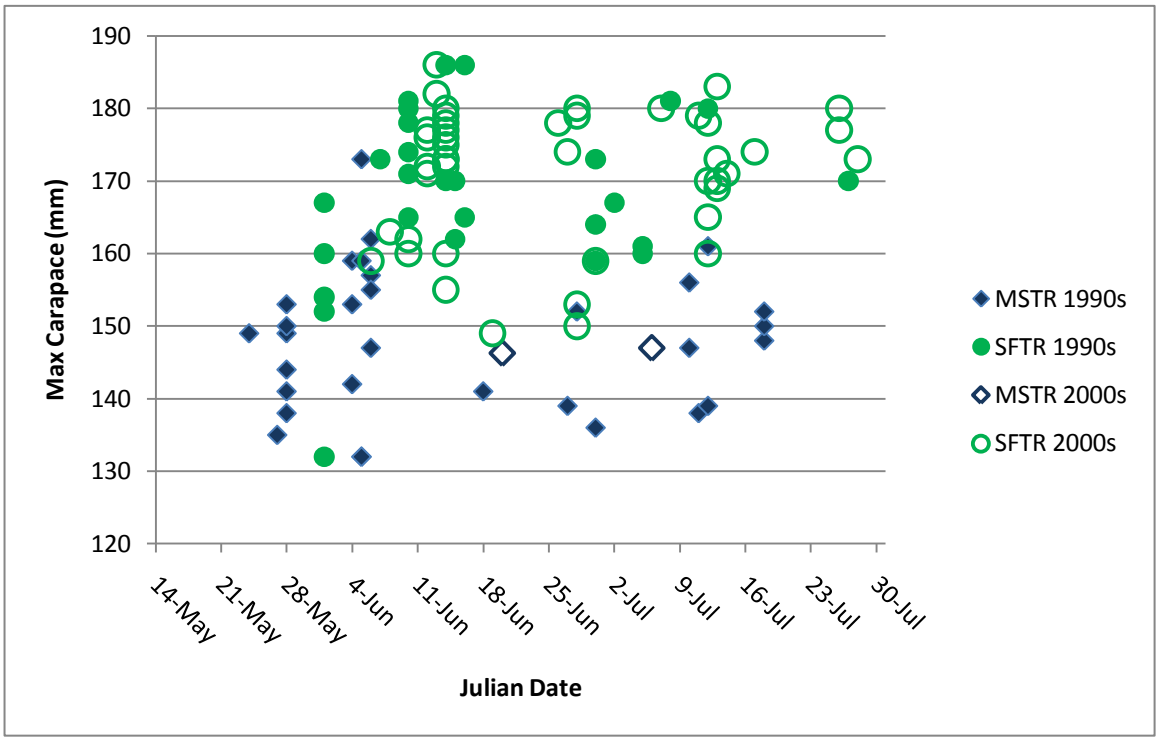


Figure 4. Gravid females encountered in the 1990s and 2000s on the two forks. Closed diamonds represent 1990s females on the MS and closed green circles are 1990s females on the SF; open blue diamonds are 2000s females on the MS and open green circles are 2000s females on the SF.

Size, Age, Growth, and Body Condition (Research Topic 2)

Aging of Turtles by Annuli Counts

In 2005-2007 we marked 568 individual turtles, 232 on the main fork and 336 on the south fork; with recaptures we logged a combined total of 1094 encounters. Plastron photos of juvenile turtles confirmed that a single growth ring was deposited each year, allowing us to use annuli counts to determine their age. In 13 cases individuals under the age of 10 were captured in early surveys and recaptured a minimum of six weeks later in the same year. In all 13 cases we found that they had been aged a year younger in the early captures relative to the later recaptures, indicating that new annuli may not become visible until later in the growing season. Examination of photos revealed most growth occurred from mid-June through August (Fig. 5).

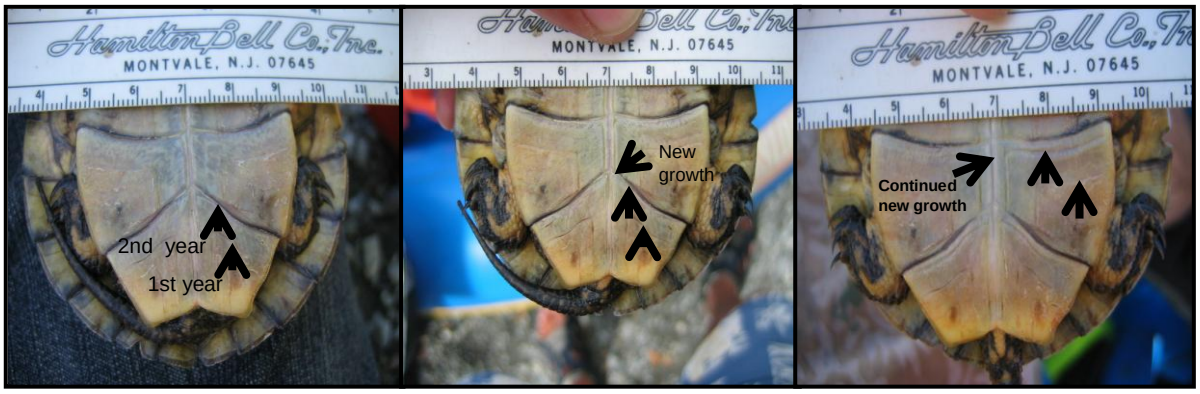


Figure 5. Plastron photos for western pond turtle #979: from left to right, first capture on 14 June 07, Max Cara 84.5mm, Age 2; second capture on 28 June 07, Max Cara 86.7mm, Age 2; third capture on 19 July 07, Max Cara 91.8mm, Age 3.

Adult Size Analysis

The analysis of adults >125 mm of known sex confirmed a significant difference in carapace length between forks , with main stem turtles significantly smaller than those of the south fork (Table 7) (Fig. 6). Between the two decades, size was relatively constant and there was not a significant interaction between decade and fork (Table 7). For both forks and decades, males were generally larger than females (Table 8) (Fig. 7).

Table 7. Three-factor analysis of variance (ANOVA) of mean carapace length (CL) for adults of known sex > 125 mm CL by fork (MS vs SF), decade (1990s vs 2000s), and sex (♂ vs ♀) with Tukey-Kramer multiple comparisons (alpha < 0.1) *0.1-0.01, **<0.000001.

Factor	DF	MSE	F	P	Multiple comparisons
Fork	1	30370.44	176.60	<0.01**	SF > MS
Decade	1	56.55	0.33	0.57	
Fork x Decade	1	353.84	2.06	0.15	
Sex	1	842.68	4.90	0.03*	♂ > ♀
Fork x Sex	1	650.42	3.78	0.05*	SF ♂, SF ♀ > MS ♂ > MS ♀
Decade x Sex	1	11.56	0.07	0.80	
Fork x Decade x Sex	1	58.33	0.34	0.56	

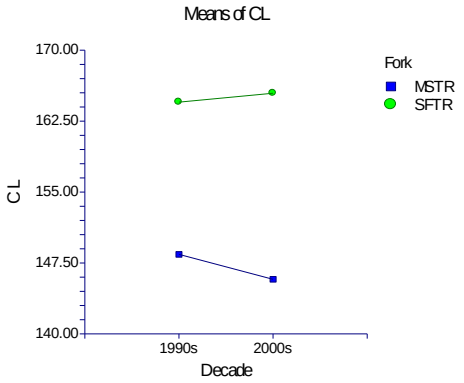
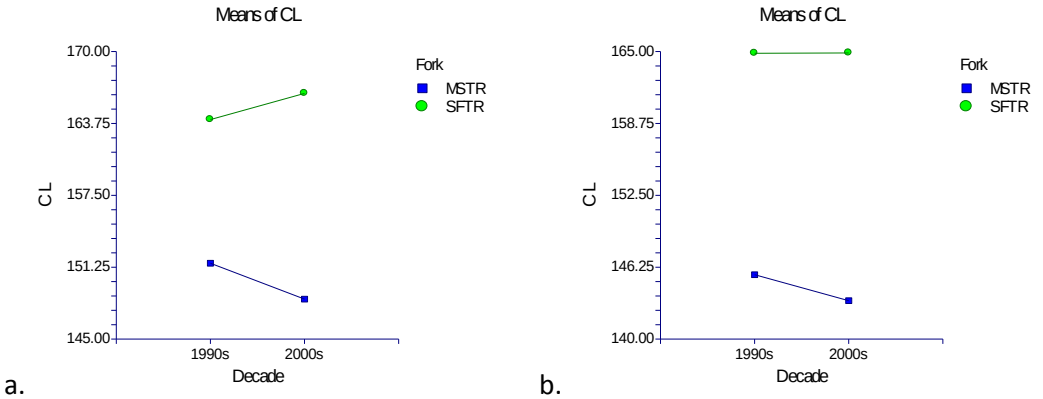


Figure 6. Comparison of mean carapace length (CL) of adults of known sex > 125 mm by fork and decade (n=489).

Table 8. Mean carapace length (CL), standard error (SE) and sample sizes for size comparisons of all adults of known sex >125 mm CL and of the upper decile by fork, decade and sex.

Factors			All Adults			Upper Decile		
Fork	Decade	Sex	CL	SE	n	CL	SE	n
MS	1990	F	145.60	1.43	84	163.00	0.86	10
		M	151.59	1.52	74	169.00	1.11	6
	2000	F	143.34	2.39	30	159.86	1.03	7
		M	148.47	2.52	27	164.10	1.22	5
SF	1990	F	164.85	1.93	46	184.33	1.57	3
		M	164.08	2.15	37	187.33	1.57	3
	2000	F	164.87	1.21	118	184.31	0.70	15
		M	166.36	1.53	73	189.86	1.03	7



a. b.

Figure 7. Comparison of mean carapace length (CL) of males (a) and females (b) of known sex > 125 mm by fork and decade (male n=211, female n=278).

Upper Decile Analysis

The top 10% of main fork turtles were significantly smaller than their south fork contemporaries (Table 8 and 9) with males significantly larger than females on both forks (Tables 8 and 9). There was a significant interaction between fork and decade; the difference between the forks was greater in the 2000s (Table 9; Fig. 8).

Table 9. Three-factor ANOVA of mean carapace length (CL) for adults in the upper decile (largest 10%) by fork (MS vs SF), decade (1990s vs 2000s), and sex (♂ vs ♀), with Tukey-Kramer multiple comparisons (alpha < 0.1) *0.1-0.01, **<0.000001.

Factor (upper decile)	DF	MSE	F	P	Multiple comparisons
Fork	1	5436.59	734.27	<0.01**	SF > MS
Decade	1	20.70	2.80	0.101	
Fork x Decade	1	74.77	10.10	<0.01**	SF ♂, SF ♀ > MS ♂ > MS ♀
Sex	1	237.72	32.11	<0.01**	♂ > ♀
Fork x Sex	1	1.93	0.26	0.61	
Decade x Sex	1	0.42	0.06	0.81	
Fork x Decade x Sex	1	12.489	1.69	0.20	

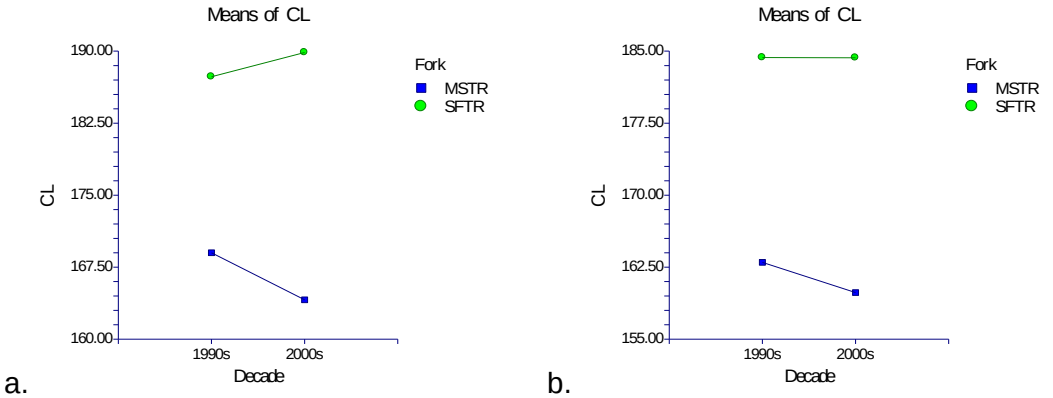


Figure 8. Means of maximum carapace length (CL) for the upper decile of males (a) and females (b) by fork and decade (male n=21, female n=35).

Size of young turtles by known age

South fork turtles aged 2-8 years (using annuli counts) were larger than main fork turtles of the same age for both decades (Table 10; Figs. 9a,b). Between the decades mean carapace length declined for the main fork, but remained relatively constant for south fork turtles (Table 10; Fig. 9c). A three-factor analysis of variance indicated significant differences for all factors and interactions except decade by age (Table 11).

Table 10. Sample size and mean carapace length (CL) for 2-8 year olds by fork and decade.

(2-8 y/o)	MS 1990s		SF 1990s		MS 2000s		SF 2000s		
Age	***n***	**CL**	***N***	**CL**	***n***	**CL**	***n***	**CL**	
2	2	52.0	16	80.1	4	64.3	26	78.1	
3	3	70.0	9	105.6	4	71.3	40	100.4	
4	9	93.1	7	113.6	6	78.5	30	114.2	
5	11	98.0	4	127.0	9	79.4	19	125.2	
6	9	94.4	13	128.2	13	84.5	12	126.9	
7	7	114.4	3	136.7	16	91.0	9	141.5	
8	8	118.4	2	133.5	28	97.5	7	143.2	
	49		54		80		143		total n=326

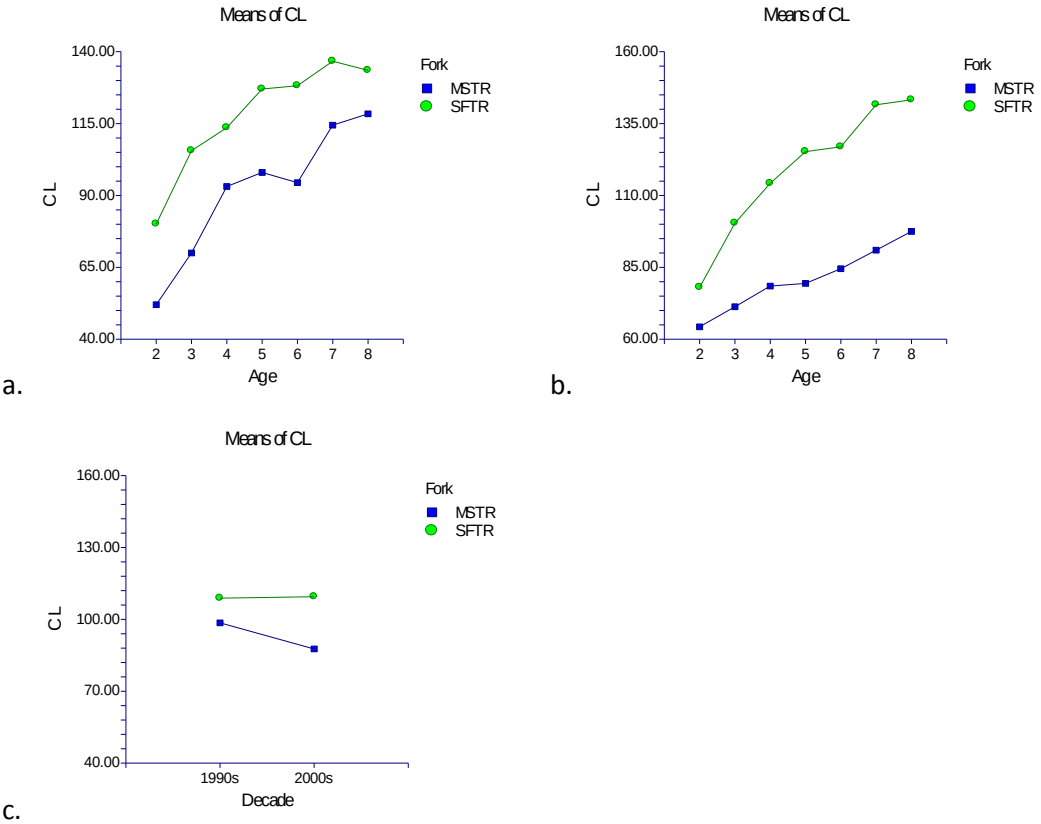


Figure 9. Mean carapace length (CL) for ages 2-8 years by fork in the (a) 1990s and (b) 2000s, and (c) changes in mean carapace lengths between decades.

Table 11. Three-factor analysis of variance (ANOVA) of mean carapace length (CL) for juvenile turtles by fork (MS vs SF), decade (1990s vs 2000s), and age (2-8), with Tukey-Kramer multiple comparisons (alpha < 0.1) *0.1-0.0001, **<0.000001.

Factor (2-8 y/o)	DF	MSE	F	P	Multiple comparisons
Fork	1	46174.88	347.64	< 0.01**	SF > MS
Decade	1	1093.90	8.24	< 0.01*	1990s > 2000s
Fork x Decade	1	1436.646	10.82	< 0.01*	SF 1990s, SF 2000s > MS 1990> MS 2000s
Age	6	9595.39	72.24	< 0.01**	8,7,6,5,4 > 3 > 2
Fork x Age	6	243.79	1.84	0.09*	SF 8-4 > SF 3, MS 8-4 > SF 2 > MS 3, MS 2
Decade x Age	6	175.07	1.32	0.25	
Fork x Decade x Age	6	454.84	3.42	< 0.01*	SF 1990s 8-5, SF 2000s 8-5 > MS 1990s 8-7, SF 2000s 4, SF 1990s 4-3 > MS b 8-4, MS a 6-4, SF a 2, SF b 3-2 > MS 1990s 3-2, MS 2000s 3-2

Growth Curves

The two growth models gave slightly different estimates; however, both indicated significant differences in growth between the two forks with a lower growth trajectory resulting in smaller sizes for young turtles (<10 yrs) on the main fork compared to the south fork (Table 12, Fig. 10).

Table 12. Growth models for main fork (MF) and south fork (SF) pond turtles <10 yrs. Models were calculated with turtles whose ages were verified by inspection of plastron photos.

River	Model Type	Estimated Models	A^a	r^2	n^b
MF	Richards	(91.45945)*(1+((1.216645)-1)*EXP(-(.52874)*(MF_Age)-(.72549))))^(1/(1-(1.21664))))	91.459	0.852	54
	von Bertalanffy	(98.35574)*(1-EXP(-(.2948787)*((MSTR_Age)-(-.96138))))	98.355	0.849	54
SF	Richards	(151.499)*(1+((.4538835)-1)*EXP(-(.371688)*(SF_Age)-(.53942))))^(1/(1-(.45388835))))	151.499	0.870	127
	von Bertalanffy	(165.3219)*(1-EXP(-(.254468)*((SFTR_Age)-(-.417794))))	165.321	0.869	127

[a] asymptotic size (mm)
[b] sample size by river

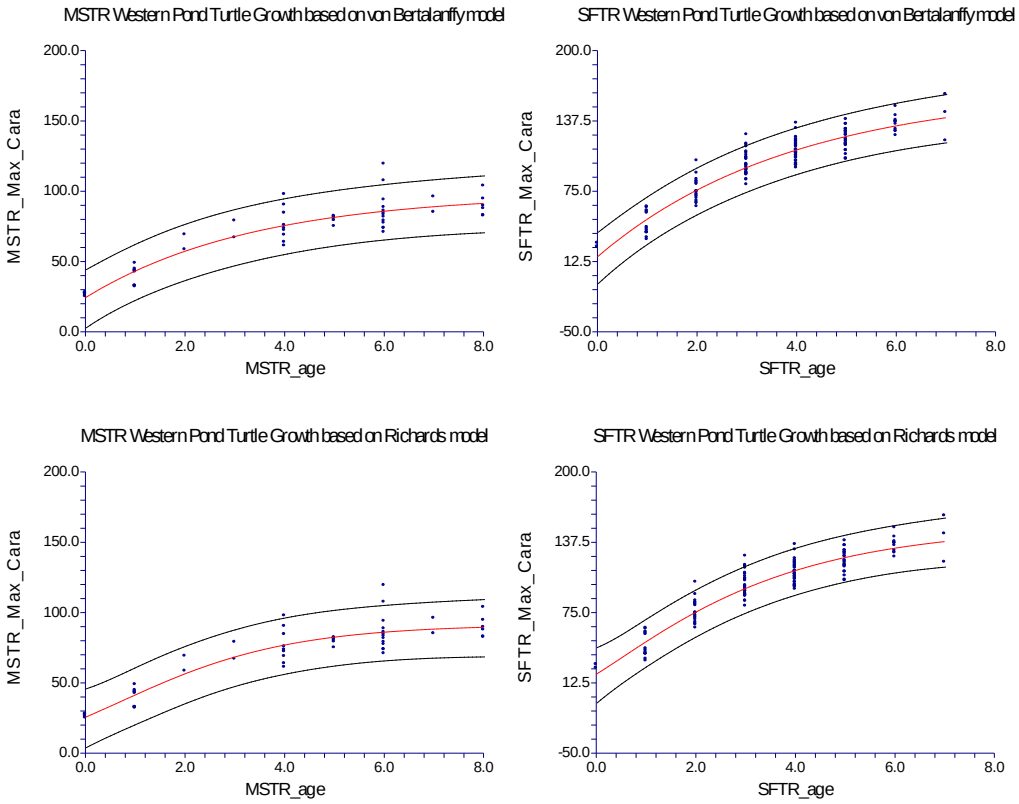


Figure 10. Growth curves for young turtles (<10 yrs) on the main fork and south fork based on von Bertalanffy (top) and Richard's (bottom) growth models.

Hatchling Growth Curves

Growth rates of first year turtles was greater on the south fork then on the main fork (Fig. 11).

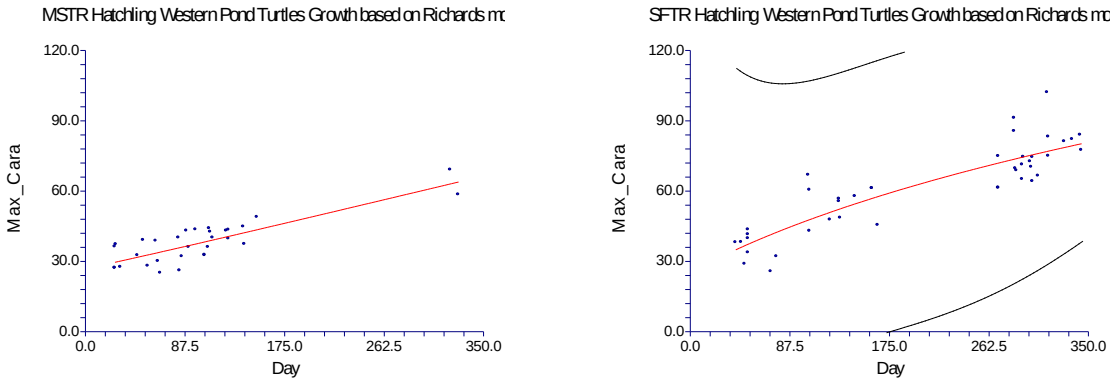


Figure 11. Growth rates for first year hatchlings based on Richard's growth model. Growth started on 01 April.

Juvenile to Adult Ratios

Based on a 125 mm carapace size cut-off to define juveniles, the ratio of adults to juveniles on the south fork remained relatively constant across decades, but changed from 78% to 51% adults on the main fork (Fig. 12). Adult male sizes also differed between the forks (Fig. 12), with adults on the main fork reaching maturity at a smaller size (Fig. 13).

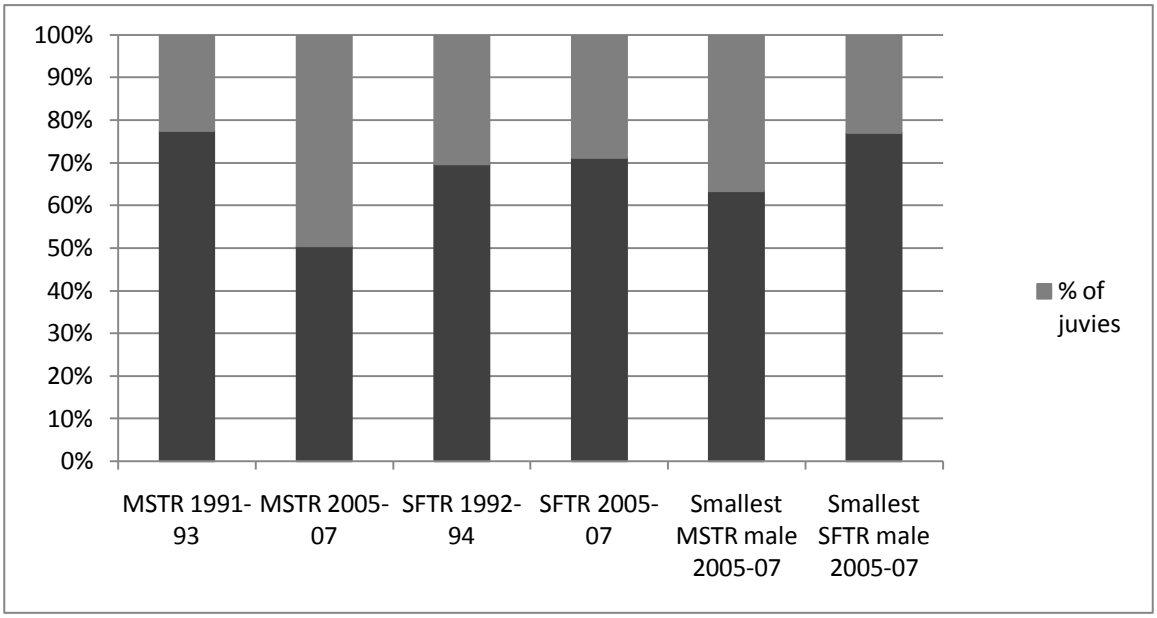


Figure 12. Percent of population represented by juveniles and adults from surveys by river fork and decade based on >125mm size cut off, and percent of population represented by each age class based on smallest male for each fork size cut off criteria for captures during the 2000s sampling period.


. b.


Figure 13. Photos showing turtles captured at each river fork; (a) main fork turtle #428 at seven years old is 80.7 mm CL and 89 g, and (b) south fork turtle #704 at six years old is 126 mm CL and 276 g.

Body Condition

Female body condition was greater on the main fork compared to the south fork in both the 1990s (t= 4.095, p = 0.0001) and in the 2000s (t = 1.94, p = 0.0551); these differences appear to be less extreme in the later decade (Fig. 14). We found no differences in body condition between forks for male turtles (1990s: t= 0.33, p = 0.7395; 2000s: t= -0.21, p = 0.8345).

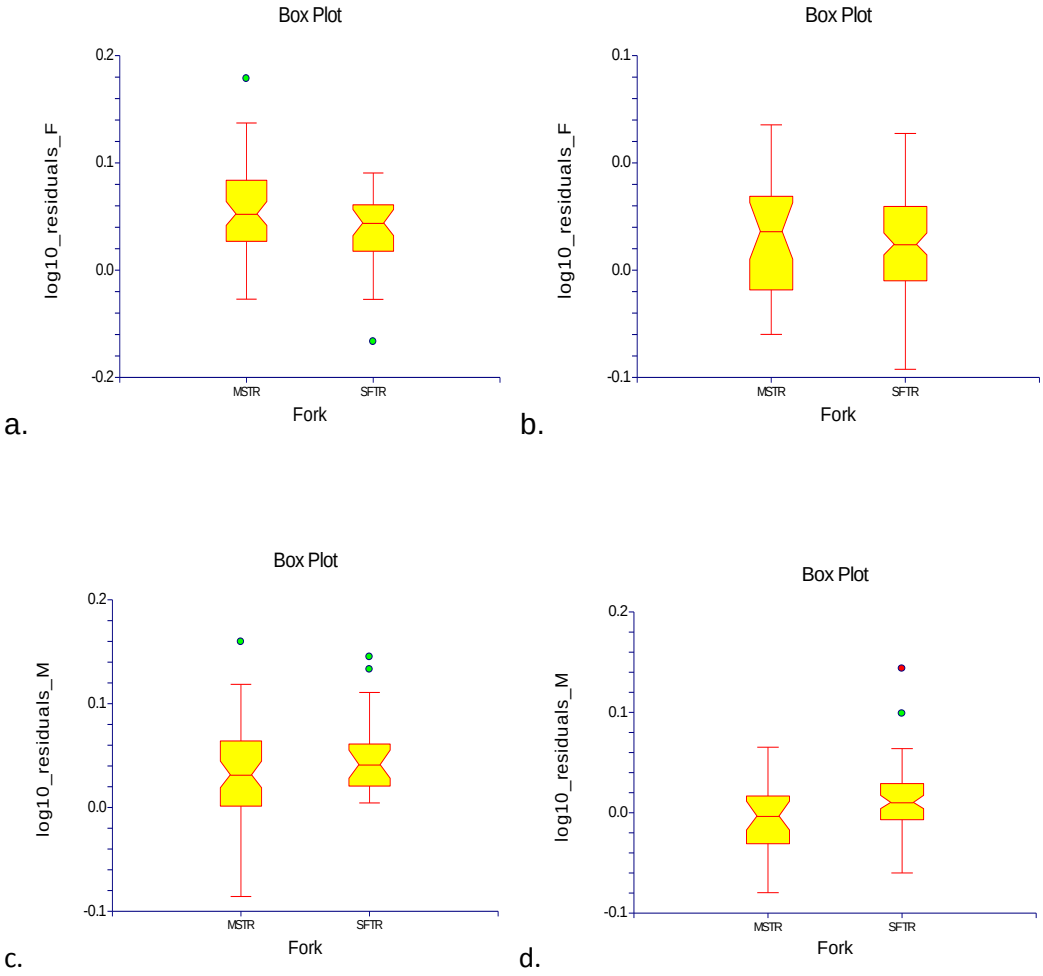


Figure 14. Box plots of residuals for body condition of females >125 mm by decade: (a) 1990s and (b) 2000s; and males >125 mm (c) 1990s and (d) 2000s.

Thermal Ecology (Research Topic 3)

Maximum water temperatures in July were used to compare with turtle temperatures to indicate thermoregulatory behaviors such as basking or seeking alternative thermal refugia. On the south fork the maximum July river temperature was ~24° C in 2005, ~27° C in 2006, and

~26° C in 2007. On the main stem fork the maximum river temperature in July was ~17° C in 2005, ~16° C in 2006, and ~18° C in 2007. This analysis indicated that main fork turtles spent significantly more time basking than those on the south fork (t= 7.20, P = 0.000) (Fig. 15).

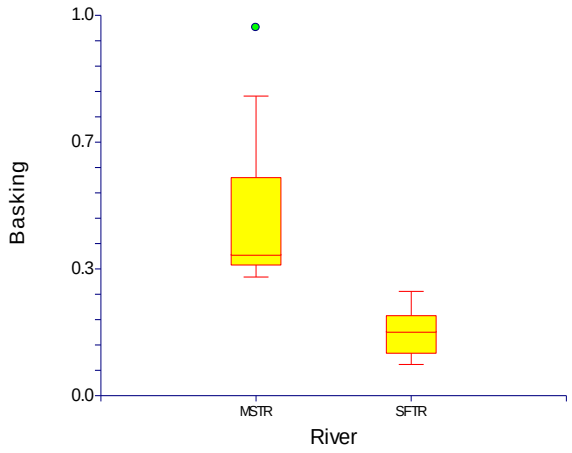


Figure 15. Proportion of time spent basking by turtles on the main fork (MF; n= 18), and south fork (SF; n=21); data are combined from three summers (2005 - 2007).

Spatial Dynamics (Research Topic 4)

The distance between furthest capture points for each recaptured turtle was the metric used to compare movements between forks, decades, and sexes (Table 13). The mean distance moved for adult males was significantly greater than adult females (Table 14). Differences in mean distances moved between forks and decades were not significant; this was also the case with the interactions between these factors (Table 14).

Table 13. Sample size, mean of maximum distance moved, and standard error by fork, decade, and sex (n=341).

Factors					
Fork	Decade	Sex	n	Mean Distance Moved (m)	SE
MS	1990	F	39	341	119.3
		M	47	710	108.7
	2000	F	65	253	92.4
		M	30	623	136.1
SF	1990	F	15	790	192.4
		M	7	543	281.7
	2000	F	94	348	76.9
		M	44	669	112.3

Table 14. Three-factor analysis of variance (ANOVA) of log-transformed maximum movement distance for adults of known sex > 125 mm CL by fork (MS vs SF), decade (1990s vs 2000s), and sex (♂ vs ♀) with Tukey-Kramer multiple comparisons (alpha < 0.1) *0.1-0.01, **<0.01.

Factor	DF	MSE	F	P	Multiple comparisons
Fork	1	0.93	2.11	0.15	
Decade	1	0.05	0.11	0.74	
Fork x Decade	1	0.49	1.11	0.29	
Sex	1	5.34	12.07	<0.01**	♂ > ♀
Fork x Sex	1	0.13	0.28	0.59	
Decade x Sex	1	0.45	1.02	0.31	
Fork x Decade x Sex	1	0.13	0.29	0.59	

The frequency distribution of movement distances (binned in 250 m increments), regardless of sex, was leptokurtic (most turtles exhibited little or no movement and few moved long distances) (Fig. 16). Sixty-four percent of female movements across years were less than 250 m; 68% of male movements exceeded 250 m. A full 80% of female movements between years were < 500 m, while 80% of the male recaptures exceeded 1250 m. Movement for turtles of unknown sex (juveniles) resembled that of the females, with 70% of movements < 250 m, and > 82% of movements < 500 m. Ten movements were > 2.5 km (range = 3121 to 6320 m). Of these ten, six were by males and four by females, with the longest movements by three females (5380, 5808, and 6320 m). The ratio of sedentary to nomadic movements was 1:2.73, indicating turtles were nearly three times as likely to stay within a 500 m zone (250 m in either direction) as they were to move beyond that distance between years.

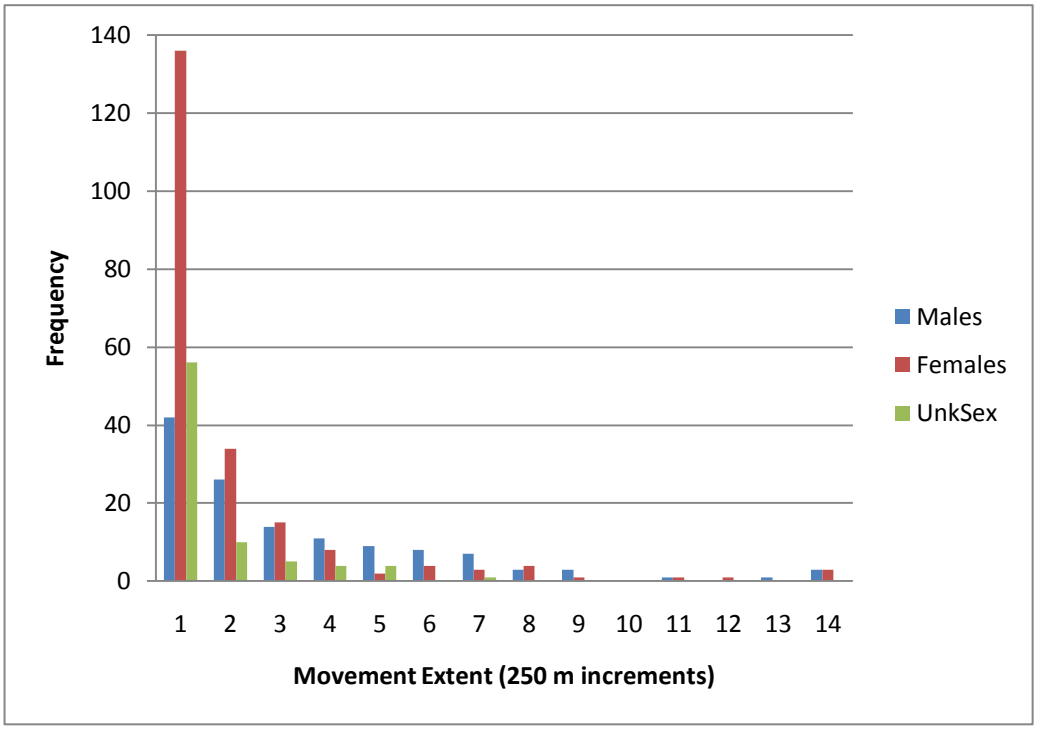


Figure 16. Frequency distribution of movement extent by male (n=128), female (n=212), and unknown sex (n=80) turtles, binned in 250 meter increments (e.g., bin 1 = 0 to 250 m; bin 2 =250 to 500m; bin 14 = 3500 m and beyond).

DISCUSSION

Demography (Research Topic 1)

Population Estimates and Densities

Population estimates using Program MARK were very close to the actual number of first time captures on each fork (MS first time capture = 232, pop est. = 220; SF first time capture = 336, pop est. = 350). Density estimates from the 2000s compared closely with those of the 1990s (Reese and Welsh 1998a); 1990s density for the main fork was 19 turtles/ha while the 2000s density was 18 turtles/ha, the south fork estimates in both decades was 13 turtles/ha. Using the more conservative approach for estimating densities by including only the eight meters of river searched during snorkel surveys, the number of turtles per hectare increases to 49 turtles/ha on the MS and 50 turtles/ha on the SF, essentially equal densities on the two forks.

Adult Survival Estimates

Annual survival estimates for adult turtles were similar on the two forks, at 95% for MS males and 96% for MS females and 96% for SF males and 97% SF females, indicating high survivorship once turtles achieve adulthood. A related species, the European pond turtle (*Emys orbicularis*), was reported to have high annual survival of adults on paired pond (lentic) sites in France (Olivier et al. 2010). At an undisturbed site female survival was 99% and male survival 85%; at the disturbed site female survival was 94% and male survival was 88% (Olivier et al. 2010). We found similar but slightly higher male and similar female survival estimates on the two forks of the Trinity compared with these two European pond turtle populations.

Adult Capture Probabilities by River

Capture and recapture probabilities were nearly identical for both sexes within each fork, but varied slightly between forks for the three primary sampling periods of the 2000s (Fig. 2); values were lower for the first two years on the south fork compared to the main fork. This may be due to more diverse habitats (deeper pools and larger substrate) available for turtles to find refuge and avoid detection on the south fork. The improved detection probabilities are likely the result of diver familiarity with turtle refuge sites by the third survey, and/ or that shallower water during a dry water year facilitated detection. The lower detection probabilities from the first to the third survey may be influenced by turtles learning to recognize and hide from approaching snorkel surveyors. Our detection probabilities are similar to the study of the European pond turtle (Olivier et al. 2010).

Operational Sex Ratios

We found operational sex ratios differed significantly from 1:1, with more females than males on both forks. However, this difference was not consistent for the main fork population; only a single analysis, that of first time captures, was significant for the main fork with the other tests showing no difference. On the south fork all five tests were significant. One other published account of adult sex ratios for this species (Gibbons 1990b) indicated that the Hayfork Creek population had more adult males (246) compared to adult females (210), but this was not significantly different from a 1:1 sex ratio. Because the SF population consistently showed a female bias we are confident that there is an actual skew in the population. The main fork population, on the other hand, appears to have a 1:1 sex ratio. The western pond turtle is a

species with temperature dependent sex (TDS) determination (Valenzuela 2004) and further study concerning sex ratios of these two populations and the mechanisms driving any differences (e.g., female skew in SF population) would be informative. A common pattern in species that demonstrate TDS is that lower to moderate incubation temperatures tend to yield more males and higher temperatures produce more female offspring (Ewert et al. 1994). Consistent with the sex ratio we found, we did find higher water temperatures on the south fork. However, it is unknown whether ambient air or water temperatures affects sex determination of *A. marmorata* in utero, as most studies of turtles have examined the effects of nest incubation temperatures on the determination of sex. None-the-less, in light of shifting climate patterns, monitoring sex ratios may be important in assessing the effects of global temperature changes on population demographics on both forks.

Gravid Females

A basic understanding of the life history trait of nesting phenology is a vital component of successfully managing a species over the long term. Our observations from data collected over the past two decades can serve to illustrate this point. The general pattern we observed is that populations on both forks have fairly long time periods when gravidity can be detected using manual palpation. This period generally lasts from late May to late July and corresponds roughly to the nesting season. The disproportionately large number of gravid females we encountered on the SF during the 2000s compared to the number we found on the MS may be an indication that differences between the two river forks are affecting reproductive output that thus have profound implications at the population level. We have considered two potential hypotheses to explain this major difference, both with possible conservation implications. The first hypothesis is that main fork females are becoming gravid earlier in the season resulting in a shift of their nesting season so that it occurs prior to our surveys dates in July of 2005-2007. The second hypothesis is that the smaller size of adult females on the MS is resulting in a delay in maturation or a departure from an annual reproductive cycle. Sorting out and confirming these hypotheses will require a focused assessment of adult female reproductive effort in order to understand potential impacts to recruitment of young turtles into the population on the main fork.

Size, Age, Growth, and Body Condition (Research Topic 2)

Our analysis indicated a declining trend in average body size of adult turtles captured on the main fork that we did not find on the south fork. Turtles are long-lived organisms and some individuals could be older than 47 years of age, so we suspect that the few older adult turtles on the main fork that were similar in size to those on the south fork may have reached adult size prior to dam construction. It is also possible that some individuals attained larger sizes by inhabiting ponds or other warmer water habitats adjacent to the main fork during their earlier growth years, thus minimizing their exposure to dam-induced changes such as a colder aquatic thermal regime. Consistent with this declining trend in adult body size, we also found that juveniles on the main fork had smaller carapace lengths than south fork turtles of comparable age. Both of these developmental differences are probably the result of slower growth rates in the colder aquatic environments of the main fork compared to the south fork (see Atkinson 1996). The growing season for juveniles corresponds to a time of substantially lower summer water temperatures when dam releases were increased in an effort to improve the salmonid fishery. Variation in body size of western pond turtles in Oregon has been attributed to differences in thermal regime between lentic and lotic habitats, though actual thermal differences were not reported (Germano and Bury 2009).

Based on our analysis, western pond turtles on the main fork are growing slower than those on the south fork (e.g., Figs. 11 and 13). We believe this difference in growth rates is a biological response to changes from the pre-dam environment, particularly the altered thermal regime and the loss of warm-water juvenile rearing habitats. Reese and Welsh (1998b) reported a reduction in suitable rearing habitat since dam construction on the main fork, specifically of shallow warmer-water margins and backwaters. Adult body size of turtles is 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. For example, the growth rate of snapping turtles (*Chelydra serpentia*) increased with warmer environmental temperatures (Galbraith et al. 1989). The effect of cooler temperatures on stream productivity (e.g., a reduction in food availability) may further reduce rate of growth and reduce 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 he later suggested that the increased growth in those populations may have been a result of increased production of lower trophic levels rather than direct temperature effects on turtle physiology (Gibbons 1970). Proximate mechanisms and ultimate long-term population-level impacts of such thermal alterations need to be further explored.

Our finding of higher body condition of female turtles on the main fork compared with those on the south fork in both decades has implications for recruitment at the population level. We believe the higher body condition of main fork females does not indicate better health (e.g., Polo-Cavia et al. 2010), but is likely a proximate response to the altered thermal regime. We suspect that colder summer water temperatures are inducing chronic stress, along with the behavioral changes (Fig. 15), and that this is restricting the allocation of resources to growth and reproduction toward compensatory lipid storage. Under environmentally challenging conditions consumed resources of turtles can be diverted to lipid storage rather than used for growth (Kozlowski et al. 2004) or reproduction (Rollinson and Brooks 2007).

Within Season Age Discrepancies

The western pond turtles that we captured early in a season and recaptured later in the same season did not show evidence of new growth until the latter part of the growing season. This phenomenon has been observed in red-eared slider turtles (*Trachemys scripta elegans*) (Stone and Babb 2005). Evaluation of growth during the active foraging period for pond turtles needs to account for the fact that there may be no evidence of new growth detected until turtles have replenished used stores of fat post- emergence from hibernation. Accounting for this period of replenishment would modify previously established growth modeling (Kozlowski and Uchmanski 1987; Fig. 17). Correlating age to a specific size (ideally the maximum size an individual can attain at a given age) can reflect the growth of individuals at a population level; our findings indicated that individuals can be assigned to two age classes during a single season depending upon when they are captured. The first assignment from an early season capture would represent the maximum size attained in the previous growing season, reflecting last year's age in a subsequent year. The second age class assignment would reflect growth that had occurred within that season based on new annuli established in that year and not present until a later recapture. Consequently, caution should be used when comparing multiple populations

that have distinct capture events for a site based on a single season visit. Care should also be taken when comparing populations from two distinct seasons with regards to using weight (mass) as an indication of health or fitness when animals after emerging from hibernation are lighter than end of the season captures when they have put on reserves in anticipation of the next hibernation event.

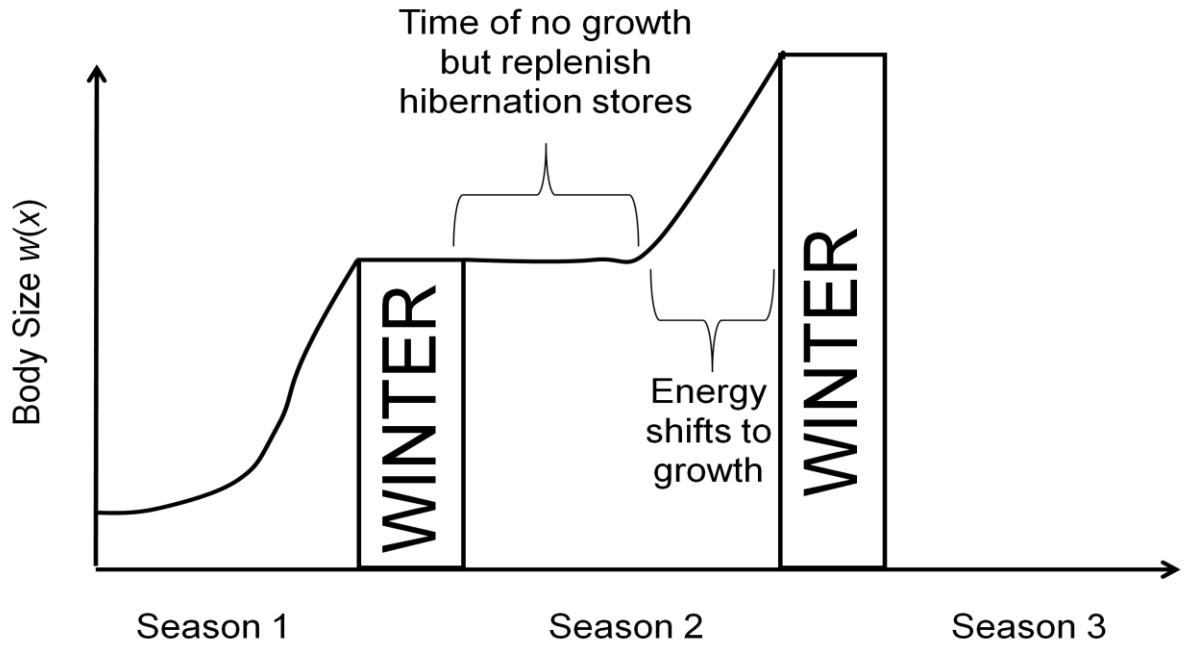


Figure 17. Theoretical shifts in resource allocations for specific life-history parameters. Turtles emerging from hibernation need to allocate early season resource provisions to replenish used hibernation stores; later resource acquisitions could then be allocated to growth. Modified from Kozlowski Figure 2 (Kozlowski 1992).

Thermal Ecology (Research Topic 3)

We believe the differences in time spent basking by turtles on the two forks is a behavioral response to the flows and related thermal regimes available along each reach. There are several mechanisms that can affect the behavior of main fork turtles in response to the managed flow releases from the Lewiston Dam. The duration of the summer flows with a 2000 cfs bench extends into early July does not follow historical (pre-dam) hydrographs for this

system. These bench flows thus may prevent the main fork channel from providing optimal environments for turtles until the flows are reduced to 450 cfs in mid-July (e.g., Poff and Zimmerman 2010). Lower water temperatures from the hypolimnetic releases from the Lewiston Dam could be affecting the main fork population by altering foraging abilities or assimilation efficiencies (see Olden and Naiman 2010). An increase in dam discharge in mid-August may have a negative impact by promoting early hibernation and over-crowding in more thermally-preferred adjacent pond habitats. These habitat modifications may also cause females to produce smaller clutches or prevent them from achieving sufficient lipid reserves to even develop ova, thus decreasing recruitment and eventually population fitness. We found turtles on the south fork still using the river channel during the month of September; however, many of turtles on the main fork had already left the river and were exhibiting over-wintering behaviors. Early departure from foraging habitats may induce additional stresses associated with a prolonged hibernation cycle. Timing and location of terrestrial hibernacula of spotted turtles (*Clemmys guttata*) were found to be important factors in over-winter survival (Litzgus et al. 1999). More research into the responses of western pond turtles to the altered flow and thermal regime in the Trinity River Basin is needed.

Spatial Dynamics (Research Topic 4)

Western pond turtles along both forks demonstrated strong site fidelity to riverine environments regardless of life stage or sex. Many individuals in this study were repeatedly detected within the same 500-m section of river, including many recaptures across the decades. Male turtles moved greater distances than female and juvenile turtles. Other studies of riverine populations have also indicated that movement of western pond turtles is limited, with males exhibiting the most extensive movements and largest home ranges (e.g., Holland 1994; Goodman 1997). In a small northwest California stream, most movements were < 500 m, though some adult turtles moved > 1 km over a three-year study period; male turtles had linear movements that were twice that of females and juveniles (Bury 1972, 1979). Reese (1996) reported juveniles had smaller aquatic home ranges compared to adults in the Trinity River during summer months.

Strong site fidelity has been documented for numerous other turtle species. Andres and Chambers (2006) used capture–recapture to investigate site fidelity in the common musk turtle (*Sternotherus odoratus*). They found that most turtles demonstrated site fidelity, with 75% of recaptures occurring at the original capture site. One hundred and forty turtles that were translocated to the opposite end of the lake moved greater distances after displacement, with some turtles returning to their original capture location over 1 km away (Andres and Chambers 2006). Cagle (1944) used capture-recapture to study home ranges of red-eared sliders (*Trachemys scripta elegans*) and painted turtles (*Chrysemys picta*) over a four-year period. He reported that site fidelity and homing were common; some turtles performed seasonal forays for nesting, mate searching, and overwintering. Pearse (1923) also used capture-recapture to study movements of painted turtles and reported that 70% of turtles did not travel during the course of the study. Litzgus and Mousseau (2004) observed annual fidelity to home ranges in spotted turtles (*Clemmys guttata*) of both sexes, finding that females utilized greater home ranges. A study of the semi-terrestrial wood turtle (*Clemmys insculpta*) movement patterns revealed strong philopatry for both sexes (Arvisais et al. 2002). Bog turtles (*Clemmys muhlenbergii*) exhibited site fidelity with no difference in home range size or movements between sexes, although males had slightly larger home ranges during the mating season (Morrow et al. 2001). A study of map turtles (*Graptemys geographica*) showed some individuals made seasonal movements, presumably migrating between seasonal foraging sites, with male movements greater than those of females (Pluto and Bellis 1988).

Some studies have suggested that freshwater turtle movement patterns may vary by life stage, season or sex, though many report no differences. The reasons that motivate individuals to either move or remain sedentary have been addressed with a number of evolutionary models based primarily on bird and mammal research. Too few studies on freshwater turtle movement exist to postulate on widespread taxonomic trends. However, turtles are long-lived and may rely on familiarity of local surroundings to efficiently locate limiting resources. Site fidelity likely influences survival and consequently individual fitness (Gibbons et al. 1990; Clemmons and Buchholz 1997). We did not examine factors that may have influenced the overall lack of movement in these pond turtles (e.g., location of nesting and overwintering sites, distribution of food resources, or habitat availability). In our study (and others above), male turtles generally

moved greater distances than females; however the longest recorded distances were travelled by females. Females may show site fidelity based on proximity to terrestrial nesting sites. Proximity to nest sites adjacent to river reaches used by females would likely infer energetic and survivorship advantages and could benefit hatchlings as well if suitable rearing habitats are nearby. Reese (1996) suggested that sporadic, long-distance movements likely constituted dispersal, which for males could be a mate searching strategy that facilitates gene flow among subpopulations and lowers chances of inbreeding.

Because our capture-recapture data were obtained by repeated surveys of specific river reaches, we likely underestimated the full extent of movements (Reese and Welsh 1997; Horton and Letcher 2008). Turtles that permanently emigrated from our sampling reaches would not have been detected, an effect that would likely be even more pronounced near the ends of the reaches. Turtles could also move long distances undetected before returning to a previous capture site. Some turtles were recaptured after several years of no detections; we have no way of knowing if these turtles went undetected or left the study reaches and returned later. We did observe some extensive movements (e.g., Reese and Welsh 1997), and other long distance movements likely went undetected; however, the majority of individuals we recaptured exhibited site fidelity to specific river segments <500 m long. Our radio-telemetry results (data not included here) also showed patterns of limited movement, offering support for the thesis that these turtles are relatively sedentary. We expected to see differences in movements across decades, in part because the method of recording the locations in the 1990s was less precise. The lack of differences in movement between decades supports our conclusion of high site fidelity even given the limited precision of the earlier spatial data.

Home range, habitat use, and movement patterns may change in response to altered conditions, whether seasonal, stochastic, or anthropogenic in nature (Galois et al. 2002). The main fork reach has been influenced by an artificial flow regime for nearly half a century. We sought to explore the possibility that movement differences could provide a relative measure of habitat quality or fragmentation. In a stable environment of marginal quality, animals are predicted to increase their movements, whereas in an unstable environment higher site fidelity is expected (Switzer 1993). Based on this theory, a difference in movement extent between the

dammed main fork and the free-flowing south fork might suggest a response to habitat alteration, but no significant difference was detected between the two forks. We did see at least one case of an individual shifting habitat use area following a stochastic habitat alteration; however, this was a male turtle on the south fork that shifted to an area upstream after the pool he had been occupying was filled with sediments by winter flood waters.

CONCLUSIONS

Overall, the populations of western pond turtles were relatively stable across the decades on both river forks which appeared to be largely due to high adult survival. However, we also saw an increase in juveniles in the 2000s relative to numbers reported in the 1990s (Reese and Welsh 1998). Our data indicated that this may be an artifact of how age classes were defined; size rather than actual maturity was used to make this determination in the 1990s. Growth rates of juveniles on the main fork were slower than those of the south fork likely as a result of colder summer water temperatures associated with post-Record-of-Decision flows (USDI 2000). We also observed significant differences in the body sizes of adults between the two forks. The higher body condition and lower reproductive output of turtles on the main fork relative to the south fork is a possible indication of differences in long-term survival for these populations. It appears that turtles on the main fork may be experiencing stress leading to their allocation of resources to lipid storage instead of growth or reproduction. Turtles in the artificially cold thermal environment of the main fork are spending more time basking than turtles on the naturally flowing south fork, yet they are still not able to achieve the average body temperatures of the turtles on the south fork. Low summer temperatures of turtles on the main fork are likely causing chronic cold stress, reducing growth and resulting in a trend of decreasing reproductive output. 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.

Our examination of western pond turtle ecology on the two forks of the Trinity River yielded results that imply the current management of the main fork is having both short- and long-term negative effects on the main fork turtle population. In addition to reducing suitable habitat (Reese and Welsh 1998b), the altered flow regime and resulting colder water temperatures are the apparent cause of the differences in key metrics of population status,

including basking behavior, growth, development, and body condition, with implications for reduced reproductive output and population fitness on the managed fork. We acknowledge that these variables can be influenced by genetic, climatic, and biotic factors, however; the proximity of these populations and the combined evidence in this report support the more parsimonious interpretation for these differences is the managed verses natural flow regime.

Management Options

Several life-history traits specific to turtles (i.e., long-lived, delayed sexual maturity, temperature dependent sex determination, and iteroparity) make conservation of these animals a challenge, but minor restoration and management adjustments can offer huge benefits. Habitat manipulations associated with restoration activities may present challenges to these sedentary animals, although they are likely capable of relocating to new sites if conditions at their home site degrade and they are provided time and access. Along a particular stretch of river, turtles tend to cluster in areas of that provide the most resources. If mechanical alteration is proposed for an area currently occupied by turtles, it may be beneficial to enhance adjacent areas first. Displaced turtles could then have access to nearby suitable areas during restoration and post-restoration site recovery. Enhancements could be relatively simple modifications to adjacent areas, ideally occurring at least one year prior to earth moving activities at restoration sites with turtles. Enhancements could include adding basking sites, opening of riparian canopy where direct sunlight is a limiting factor, or deepening of pools and creating underwater refuges. Impacts on social structure are unknown and may not be an issue; further analysis and ongoing observations of populations may provide insight on any impacts to social structure.

The decreasing trend in body size raises concern for the long-term viability of the main fork population, but it may also provide clues to guide interdisciplinary research and adaptive management. Increased habitat heterogeneity can provide environmental gradients that may allow turtles to seek micro-habitats to foster specific life history functions. The TRRP is developing restoration efforts that will influence some of the historical floodplains and associated aquatic habitats once contained along the Trinity River under pre-dam conditions. Aquatic thermal diversity is an important factor and should be considered among any restoration goals. Shallow edgewaters, backwaters, floodplain ponds and other aquatic habitats

off the main channel can provide warmer thermal refuges for western pond turtles that could off-set the altered thermal regime of the main fork. A difficult challenge will be establishing historical aquatic habitat conditions that will benefit turtles, other herpetofauna, and other riparian associated wildlife in the main fork basin without creating backwater "stranding" pools that may negatively impact salmonid species or facilitate colonization by exotic species (e.g., bullfrogs) (see Beechie et al. 2010).

Timing and duration of flows from the Lewiston Dam may directly impact the main fork turtle population. Late summer flow releases in August to assist relief of river conditions in the Klamath River (below Weitchpec) may prompt main fork turtles to leave the river and seek over-wintering habitat earlier than the norm. Extended hibernation may cause negative long-term effects on the condition of these turtles by creating a stressful demand on body fat reserves. Insufficient lipid reserves may cause direct mortality or may prevent normal egg development and consequently lower recruitment, negatively affecting population fitness.

Future Research Needs

1. Further examine the responses of western pond turtles to altered flow regime on the main fork;
2. Examine the use of restoration sites, including microhabitat and alternative thermal regimes;
3. Monitor nesting season/female reproduction efforts (does it differ between forks and what are the implications for populations in the future?);
4. Research reproductive output over time on both forks;
5. Examine whether sex determination of embryos (*in utero*) is affected by river water temperatures;
6. Monitor changes in turtle sex ratios as an indicator of changing thermal regimes resulting from flow manipulations and possibly global warming.
7. The effects of flow management on site fidelity is poorly understood and in need of further research.

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Literature Cited

Andres, M.K. and R.M. Chambers. 2006. A test of philopatry by common musk turtles. American Midland Naturalist 156:45-51.

Arvisais, M., J.C., Bourgeois, E., Lévesque, C., Daigle, D., Masse, and J. Jutras. 2002. Home range and movements of a wood turtle (*Clemmys insculpta*) population at the northern limit of its range. Canadian Journal of Zoology 80:402-408

Ashton, R.E. and P.S. Ashton. 2008. The Natural History and Management of the Gopher Tortoise *Gopherus polyphemus* (Daudin). Krieger Publishing, Malabar Florida. Pp. 275.

Atkinson, D. 1996. Ecotherm life-history responses to developmental temperature. *In*: I.A. Johnston and A.F. Bennett (Eds.). Animals and Temperature: Phenotypic and Evolutionary Adaption. Society for Experimental Biology, Seminar Series 59. Cambridge University Press, Cambridge.

Beechie, T.J., D.A. Sear, J.D. Olden, G.R. Pess, J.M. Buffington, H. Moir, P. Roni, and M.M. Pollock. 2010. Process-based principles for restoring river ecosystems. Bioscience 60:209-222.

Bondi, C.A. 2009. A Comparison of Western Pond Turtle (*Emys marmorata*) Movements in Perennial and Intermittent Portions of a Northwestern California River System. Unpublished Thesis, Humboldt State University, Arcata, California.

Burnham, K. and D. Anderson. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Bury, R.B. 1972. Habits and home range of the Pacific pond turtle, *Clemmys marmorata*, in a stream community. Dissertation, University of California, Berkeley.

Bury, R.B. 1979. Population ecology of freshwater turtles. Pp. 571-602 *in*: M. Harless and H. Morlock (eds). Turtles: Perspectives and Research. Wiley Interscience, New York, New York.

Bury, B. and D. Germano. 1998. Annual deposition of scute rings in the western pond turtle, *Clemmys marmorata*. Chelonian Conservation and Biology 3(1):108-109.

Bury, R.B. and D.J. Germano. 2008. *Emys marmorata* (Baird and Girard 1852) -- Western Pond Turtle, Pacific Pond Turtle. Rhodin AGJ, Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., and Iverson, J.B. (Eds.), editor: Chelonian Research Monographs 001.1-001.9 p.

Bury, R.B. and J.H. Wolfheim. 1973. Aggression in free-living pond turtles (*Clemmys marmorata*). Bioscience 23(11):659-662.

Bury, R.B, D.J. Germano, and G.W. Bury. 2010. Population structure and growth of the turtle *Actinemys marmorata* from the Klamath–Siskiyou Ecoregion: age, not size, matters. Copeia 2010 (3):443-451.

Cadi, A. and P. Joly. 2003. Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red-eared slider (*Trachemys scripta*). Canadian Journal of Zoology 81:1392-1398.

Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170-72.

Cagle, F.R. 1944. Home range, homing behavior, and migration in turtles. Misc. Publ. Mus. Zool. Univ. Mich. 61: 1-33.

Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge, U.K.

Clarkson, R.W. and M.R. Childs. 2000. Temperature effects of hypolimnial-release dams on early life stages of Colorado River Basin big-river fishes. Copeia 2000(2):402-412.

Clemmons, J.R. and R. Buchholz. 1997. Linking conservation and behavior. *In* Behavioral Approaches to Conservation in the Wild. J.R. Clemmons and R.Buchholz (Eds.). Cambridge University Press, Cambridge U.K. Pp. 382.

Congdon, J.D. and J.W. Gibbons. 1983. Relationships of reproductive characteristics to body size in *Pseudemys scripta*. Herpetologica 39(2):147-151.

Congdon, J.D. and J.W. Gibbons. 1985. Egg component and reproductive characteristics of turtles: relationships to body size. Herpetologica 41(2):194-205.

Congdon, J.D. and J.W. Gibbons. 1987. Morphological constraint on egg size: a challenge to optimal egg size theory? Proceedings of the National Academy of the Sciences 84:4145-4147.

Cooch, E. and G. White. 2007. Program MARK --- a gentle introduction. Available at http://canuck.dnr.cornell.edu/mark/.

Ernst, C.H. and R.W. Barbour. 1989. Turtles of the World. Washington: Smithsonian Institute Press, Pp.313.ESRI. 2008. ArcGIS 9.2. Environmental Systems Research Institute, Inc. Redlands, California.

Ewert, M.A., D.R. Jackson, C.E. Nelson. 1994. Patterns of temperature-dependent sex determination in turtles. Journal of Experimental Zoology 270(1):3–15.

Ewert, M.A., R.E. Hatcher, J.M. Goode. 2004. Sex determination and ontogeny in *Malacochersus tornieri*, the Pancake Tortoise. Journal of Herpetology, 38(2):291-295.

Ferner, J.W. 1979. A review of marking techniques for reptiles and amphibians. SSAR, Herpetol. Circ. No. 9

Galbraith, D.A., R.J. Brooks, and M.E. Obbard. 1989. The influence of growth rate on age and body size at maturity in female snapping turtles (*Chelydra serpentia*). Copeia 1989(4):896-904.

Galois, P., M. Leveille, L. Bouthillier, C. Daigle, and S. Parren. 2002. Movement patterns, activity, and home range of the eastern spiny softshell turtle (*Apalone spinifera*) in northern Lake Champlain, Quebec, Vermont. Journal of Herpetology 36(3):402-411.

Germano, D.J. and R.B. Bury. 1998. Age determination in turtles: evidence of annual deposition of scute rings. Chelonian Conservation and Biology 3:123-132.

Germano, D.J. and R.B. Bury. 2009. Variation in body size, growth, and population structure of *Emys marmorata* from lentic and lotic habitats in southern Oregon. Journal of Herpetology 43(3):510-520.

Gibbons, J.W. 1967. Variation in growth rates in three populations of the painted turtle, *Chrysemys picta*. Herpetologica 23:296-303.

Gibbons, J.W. 1970. Reproductive dynamics of a turtle (*Pseudemys scripta*) population in a reservoir receiving heated effluent from a nuclear reactor. Canadian Journal of Zoology 48(4):881-885.

Gibbons, J.W., R.D. Semlitsch, J.L. Greene, and J.P. Schubauer. 1981. Variation in age and size at maturity of the slider turtle. American Naturalist 117:841-845.

Gibbons, J.W. 1990a. Life History of the Slider Turtle. Smithsonian Institute Press, Washington, D.C.

Gibbons, J.W. 1990b. Sex ratio and their significance among turtle populations. Gibbons, J.W., editor. Washington, D.C.: Smithsonian Institution Press. 171-182 p.

Gibbons, J.W., J.L. Greene, and J.D. Congdon. 1990. Temporal and spatial movement patterns of sliders and other turtles. Pp. 201–215 *in*: Life History and Ecology of the Slider Turtle. J.W. Gibbons (Ed.). Smithsonian Institution Press, Washington, DC.

Goodman, R.H. 1997. The biology of the southwestern pond turtle (*Clemmys marmorata pallida*) in the Chino Hills State Park and the west fork of the San Gabriel River. Master's

thesis, California State Polytechnic University, Pomona, CA. 81 pp.

Goodman, R.H., Jr. and G.B. Rathbun. 2000. Aquatic home range of female western pond turtles, *Clemmys marmorata*, at two sites in Southern California. Chelonian Conservation and Biology 3(4):743-745.

Goodman, R.H., Jr. and G.R. Stewart. 2002. Aquatic home ranges of female western pond turtles, *Clemmys marmorata*, at two sites in Southern California. Chelonian Conservation Biology 3(4):741-745.

Grayson, K.L and M.E. Dorcas. 2004. Seasonal temperature variation in the painted turtle (*Chrysemys picta*). Herpetologica 60(3):325-336.

Hampton, M.A. 1995. Current status of fish habitat. Pp. 4-6 *in* R. L. Ridenhour (ed.), Proceedings from Trinity River Restoration Program Colloquium. American Fisheries Society. Weaverville, California.

Hintze, J. 2004. NCSS & PASS. Number Cruncher Statistical Systems. Kaysville, Utah. www.ncss.com

Holland, D.C. 1994. The western pond turtle: Habitat and history. Final Report DOE/BP-62137 Bonneville Power Administration, U.S. Dept. Energy and Wildlife Diversity Program, Oregon Department of Fish and Wildlife, Portland, Oregon. Pp. 302.

Horton, G.H. and B.H. Letcher. 2008. Movement patterns and study area boundaries: influences on survival estimation in capture-mark-recapture studies. Oikos 117:1131-1142.

Huey, R.B. and J.G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in ecology and evolution 4(5):131-135.

Huey, R.B. and D. Berrigan. 2001. Temperature, demography, and ectotherm fitness. American Naturalist 158:204-210.

Innes, R.J., K.J. Babbitt, and J.J. Kanter. 2008. Home range and movement of Blanding's turtles (*Emydoidea blandingii*) in New Hampshire. Northwestern Naturalist 15(3):431-444.

Iverson, J.B. 1992. Correlates of reproductive output in turtles (Order Testudines). Herpetological Monographs, Vol. 6:25-42.

Iverson, J.B., H. Higgins, A. Sirulink, and C. Griffiths. 1997. Local and geographic variation in the reproductive biology of the snapping turtle (*Chelydra serpentia*). Herpetologica 53(1):96-117.

Jennings, M.R. and M.P. Hayes. 1994. Amphibian and reptile species of special concern in California. Rancho Cordova, CA: California Department of Fish and Game.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563-578.

Korman, J., M. Kaplinski, J.E. Hazel III, and T.S. Melis. 2005. Effects of the experimental fluctuating flows from Glen Canyon Dam in 2003 and 2004 on early life stages of rainbow trout in the Colorado River, Grand Canyon. Final report, Cooperative agreement no. 04WRAG0006, modification no. 002.

Kozlowski, J. 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. Trends in Ecology & Evolution 7:15-19.

Kozlowski, J. and J. Uchmanski. 1987. Optimal individual growth and reproduction in perennial species with interdeterminate growth. Evolutionary Ecology 1(3):214-230.

Kozlowski, J., M. Czarnoleski, and M. Danko. 2004. Can optimal resource allocation models explain why ectotherms grow larger in cold? Integrated Comparative Biology 44:480-493.

Lind, A.J., R.A. Wilson, and H.H. Welsh, Jr. 1996. The effect of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylii*) in Northwestern California. Herpetological Review 27(2):62-67.

Litzgus, J.D. and R.J. Brooks. 1998. Growth in a cold environment: body size and sexual maturity in a northern population of spotted turtles, *Clemmys guttata*. Canadian Journal of Zoology 76:773-782.

Litzgus, J.D. and T.A. Mousseau. 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): Implications for management. Copeia 2004(4):804-817.

Litzgus, J.D., J.P. Costanzo, R.J. Brooks, and R.E. Lee, Jr. 1999. Phenology and ecology of hibernation in spotted turtles (*Clemmys guttata*) near the northern limit of their range. Canadian Journal of Zoology 77:1348-1357.

Lubcke, G.M. and D.S. Wilson. 2007. Variation in shell morphology of the western pond turtle (*Emys marmarota* Baird and Girard) from three aquatic habitats in Northern California Size and shape variation among three populations. Journal of Herpetology 41:107-114.

Magilligan, F.J. and K.H. Nislow. 2005. Changes in hydrologic regime by dams. Geomorphology 71:61-78.

McBain, B. and W. Trush. 2000. Summary of the United States Secretary of Interior Record of Decision, December 19, 2000. Trinity River Restoration Program, Weaverville, California.

Morrow, J.L., J.H. Howard, S.A. Smith, and D.K. Poppel. 2001. Home range and movements of the bog turtle (*Clemmys muhlenbergii*) in Mayland. Journal of Herpetology 35(1):68-73.

Olden, J.D. and R.J. Naiman. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology 55:86-107.

Olivier, A.C. Barbraud, E. Rosecchi, C. Germain, and M Cheylan. 2010. Assessing spatial and temporal population dynamics of cryptic species: an example with the European pond turtle. Ecological Applications, 20(4): 993–1004

Pearse, A.S. 1923. The abundance and migration of turtles. Ecology 4(1):24-28.

Pluto, T.G. and E.D. Bellis. 1988. Seasonal and annual movements of riverine map turtles, *Gratempys geographica*. Journal of Herpetology 22(2):152-158.

Poff, N. L. and J. K. H. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biology 55:194-205.

Polo-Cavia, N., P. Lopéz, and J. Martén. 2009. Interspecific differences in heat exchange rates may affect competition between introduced and native freshwater turtles. Biological Invasions 11:1755-1765.

Polo-Cavia, N., T. Engstrom, and J. Martén. 2010. Body condition does not predict immunocompetence of western pond turtles in altered versus natural habitats. Animal Conservation 13:256-264.

Reese, D.A. 1996. Comparative demography and habitat use of Western pond turtles in northern California: The effects of damming and related alterations PhD Dissertation, University of California at Berkely. Pp. 253. http://www.fs.fed.us/psw/rsl/projects/wild/reese/reese4.pdf

Reese, D.A. and H.H. Welsh, Jr. 1997. Use of terrestrial habitat by Western Pond Turtles, *Clemmys marmorata*: Implications for management, Proceedings of Conservation, Restoration, and Management of Tortoises and Turtles. International Conference, New York Turtle and Tortoise Society, pp 352-357.

Reese, D.A. and H.H. Welsh, Jr. 1998a. Comparative demography of *Clemmys marmorata* populations in the Trinity River of California in the context of dam-induced alterations. Journal of Herpetology 32(4):505-515.

Reese, D.A. and H.H. Welsh, Jr. 1998b. Habitat use by western pond turtles in the Trinity River, California. Journal of Wildlife Management 62(3):842-853.

Ricklefs, R.E. 1990. Ecology. W.H. Freeman and Company, New York.

Robinson, A.T. and M.R. Childs. 2001. Juvenile growth of native fishes in the Little Colorado River and in a thermally modified portion of the Colorado River. North American Journal of Fisheries Management 21:809-815.

Rollinson, N. and R.J. Brooks. 2007. Proximate constraints on reproductive output in a northern population of painted turtles: an empirical test of the bet-hedging paradigm. Canadian Journal of Zoology 85:177-184.

Rowe, C.L. 2008. "The calamity of so long life": life histories, contaminants, and potential emerging threats to long-lived vertebrates. Bioscience 58:623-631.

Rowe, J.W., K.A. Coval, and M.R. Dugan. 2005. Nest placement, nest-site fidelity and nesting movements in midland painted turtles (*Chrysemys picta marginata*) on Beaver Island, Michigan. American Midland Naturalist 154:383-397.

SAS Version 9.2. 2008. SAS Institute Inc., Cary, North Carolina, USA.

Scott Jr. N.J., G.B. Rathbun, T.G. Murphey, and M.B. Harker. 2008. Reproduction of Pacific pond turtles (*Emys marmorata*) in coastal streams of central California. Herpetological Conservation and Biology 3(2):143-148.

Selcer, K.W. 1990. Egg-size relationships in a lizard with fixed clutch size: variation in a population of the Mediterranean gecko. Herpetologica 46(1):15-21.

Sexton, O.J. 1959. A method of estimating the age of painted turtles for use in demographic studies. Ecology 40(4):716-718.

Stearns, S.C. and J.C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40(5):893-913.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford. Pp. 249.

Stevenson, R.D. 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. The American Naturalist 125(1):102-117.

Stone, P.A. and M.E. Babb. 2005. A test of the annual growth line hypothesis in *Trachemys scripta elegans*. Herpetologica 61(4):409-414.

Swingland, I.R. and M.J. Coe. 1979. The natural regulation of giant tortoise populations on Aldabra Atoll: recruitment. Philosophical Transactions of the Royal Society of London 286B:177-188.

Switzer, P.V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533-555.

Tilman, D., R.M. May, C.L. Lehman, and M.A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65-66.

Trush, W.T., S.M. McBain, and L.B. Leopold. 2000. Attributes of an alluvial river and their relation to water policy and management. Proceeding of the National Academy of Sciences of the United States of America. 97:11858-11863.

Underwood, A.J. 1997. Experiments in Ecology. Cambridge University Press. Cambridge, UK.

United States Department Interior (USDI). 2000. Record of Decision for the Trinity River Mainstem Fishery Restoration Final Environmental Impact Statement/Environmental Impact Report. United States Department of the Interior, Weaverville, California, December.

USDA-FSA-APFO. 2005. Aerial Photography Field Office, 20050307, NAIP Digital Georectified Image: USDA_FSA_APFO Aerial Photography Field Office, Salt Lake City, Utah.

Valenzuela, N. 2004. Temperature-dependent sex determination. Pp. 211–227 *in*: Deeming, D.C. (Ed.), Reptilian Incubation: Environment, Evolution and Behavior. Nottingham University Press, Nottingham.

White, G.C. 2009. Program MARK: Mark and recapture parameter estimation, version 5.1. Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO.

Wilson, D., C.R. Tracy, and C.R. Tracy. 2003. Estimating age of turtles from growth rings: a critical evaluation of the technique. Herpetologica 59(2):178-194.