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Comparative Demography of *Clemmys marmorata* Populations in the Trinity River of California in the Context of Dam-induced Alterations

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ABSTRACT.-Western pond turtle (*Clemmys marmorata*) populations were examined on two forks of the Trinity River in northern California, one of which is subject to the impacts of damming and one of which is free-flowing. Mark-recapture was conducted over a three-year period for each population, and the Jolly-Seber model was used to estimate population size. Size/age structures were compared with reference to potential impacts of damming on this species. The density of populations (turtles/ha) on the dammed fork (mainstem Trinity) did not differ significantly from that on the undammed fork (south fork Trinity). However, both populations were much sparser than western pond turtle populations elsewhere. Higher-order streams, in general, do not appear to support high densities of western pond turtles, possibly because of the sparse distribution of resources. The mainstem population had an age structure dominated by adults relative to a population with a known stable age distribution, suggesting that damming of the mainstem Trinity may have negatively impacted juvenile turtles.

Populations of western pond turtles *(Clemmys marmorata)* have experienced declines throughout their range (Holland, 1992; Holland and Bury, 1998). Many of these declines can be attributed to habitat alteration resulting from agricultural development and urbanization. Dams and other water diversion structures, for example, have altered aquatic habitats throughout California. Specific impacts include conversion of lotic to lentic water, reduction in water quantity and quality, and changes in flow regimes. The mainstem Trinity River, dammed in 1963, has changed dramatically as a result. Slow-moving edgewater habitats have been eliminated, riparian vegetation has expanded and encroached on the banks, and seasonally flooded marshes have become dry. Overall, the river has become more channelized with straighter edges and a lower diversity of depths and flows (Hampton, 1995). These environmental changes have been implicated in the radical decline of a native frog species in the Trinity system (Lind et al., 1996).

Little is known about the potential impacts of dam-induced alterations on western pond turtle populations. Comparison of population status in the dammed mainstem Trinity (upstream of its north fork confluence) and the undammed south fork offers an opportunity to assess these impacts. These adjacent forks of the river are similar in flow volume, channel size, vegetation, and land-use history. The south fork Trinity, with its natural alternation of riffles and deep pools, resembles the mainstem in its pre-dam condition. On the mainstem Trinity, habitats preferred by western pond turtles were probably more abundant prior to installation of the dam (Reese, 1996). Several of the downstream changes produced by the dam, including reduction of water temperature, increased sedimentation, and decreased range of flow velocities (cf. Ligon et al., 1995; Mount, 1995), have decreased the quantity and quality of suitable aquatic habitat for this species. Ultimately, a decrease in habitat suitability manifests in demographic parameters, such as reduced population size, altered age structure, or lower growth rates. For example, elimination of shallow, slow-moving waters on which hatchlings depend (Reese, 1996; Holland and Bury, 1998) might create a skewed age distribution dominated by adults. A decrease in water temperature might reduce growth and / or juvenile survivorship. Although we have no historical information on densities of turtles at either the south fork or mainstem site, we can speculate that, due to their similarity, they may have historically hosted turtle populations with similar attributes.

MATERIALS AND METHODS

Study Sites.-The mainstem study site consists of a 63-km section of river between the Lewiston/ Trinity dams and the confluence with the North Fork Trinity (Fig. 1). Wilson et al. (unpubl. data) divided this section into 16 unequal length segments, hereafter referred to as reaches. Our demography study occurred along three of these reaches (reaches 3, 10, and 11; Fig. 1),

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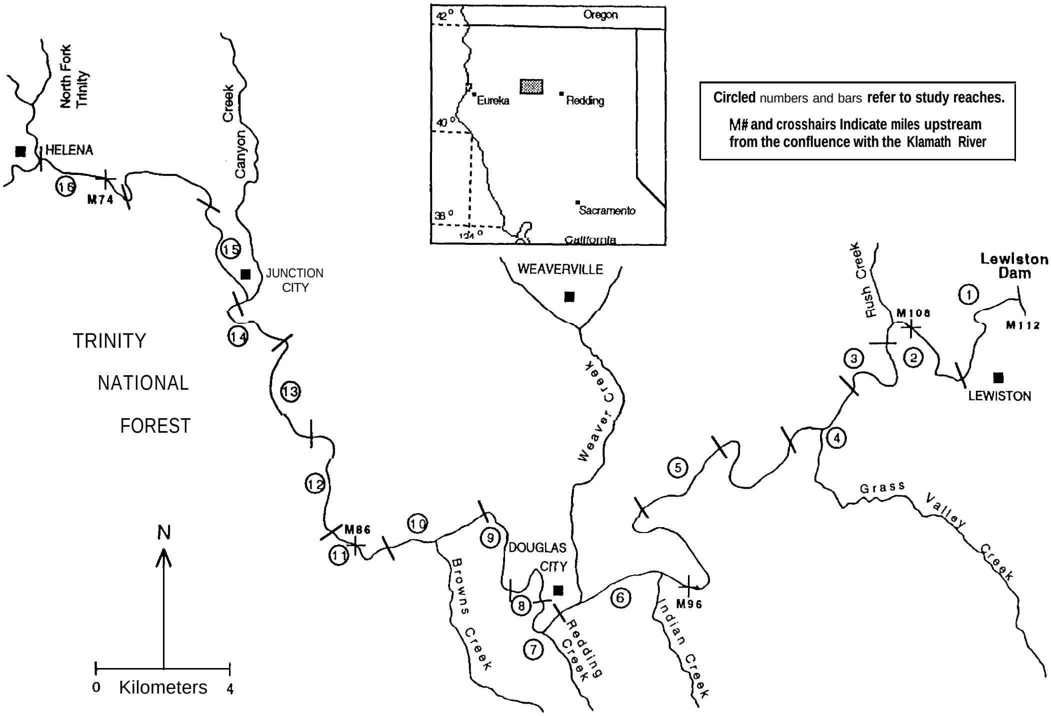

FIG. 1. Location of western pond turtle study reaches along the mainstem Trinity River, Trinity County, California.

which varied from 2.3 to 2.7 km in length and totalled 7.5 km. The mainstem reaches were selected to contain a range of turtle densities, based on earlier surveys. The south fork study site consists of a 15.6-km stretch of river between Surprise Creek and Sandy Bar, divided into four reaches, ranging from 2.3 to 5.7 km in length (reaches 1, 2, 3, and 4; Fig. 2). The inclusion of multiple reaches along each fork assured the sampling of a wide range of habitat conditions. At both study sites, the beginnings and ends of reaches were defined on the basis of access points, particularly on the south fork where road access is limited.

While the south fork is undammed, all the mainstem reaches were downstream of the Lewiston/ Trinity dam and thus subject to its influence. The dam was constructed in the early 1960s, after which fish and wildlife mitigations were addressed with a minimum flow requirement of 150 cubic feet per second. Declines in anadromous fish (primarily salmonids) were subsequently detected, as well as changes in channel morphology, prompting the implementation of a schedule of increased flow releases (USDI Fish and Wildlife Service, 1995; Unpubl. data from Trinity River flow evaluation, California water years 1942-1946, 1959-1961, 1964-1983, 1987-1992; Lewiston gaging station, Trinity Co., CA). The upper reaches are most impacted by the controlled flows; further downstream, feeder creeks contribute natural, variable flows.

The study sites otherwise share similar characteristics. The mainstem at the north fork drains an area of 2968 km^2; the south fork at its mouth drains an area of 2460 km^2. The south fork has an average annual flow of 1.1 million acre-feet (California Dept. of Water Resources, unpubl. data), which is comparable to the average annual flow of the mainstem at Lewiston before the dam was installed (1.2 million acre-feet: Lind et al., 1996). The upland habitat of both study sites may be categorized as montane hardwood-conifer or montane hardwood on north-facing and south-facing slopes, respectively (see Reese [1996] for a detailed description).

Mark-Recapture.-At the mainstem, a total of nine rounds of mark-recapture occurred on reaches 10 and 11, two during 1991 and 1992 and five during 1993. Due to logistical constraints, reach 3 was only sampled during 1992-1993, yielding a total of seven rounds of capture. At the south fork, a total of nine rounds of mark-recapture occurred on reaches 1, 3, and 4, four during the first year, two during the second year, and three during the third year. Due to

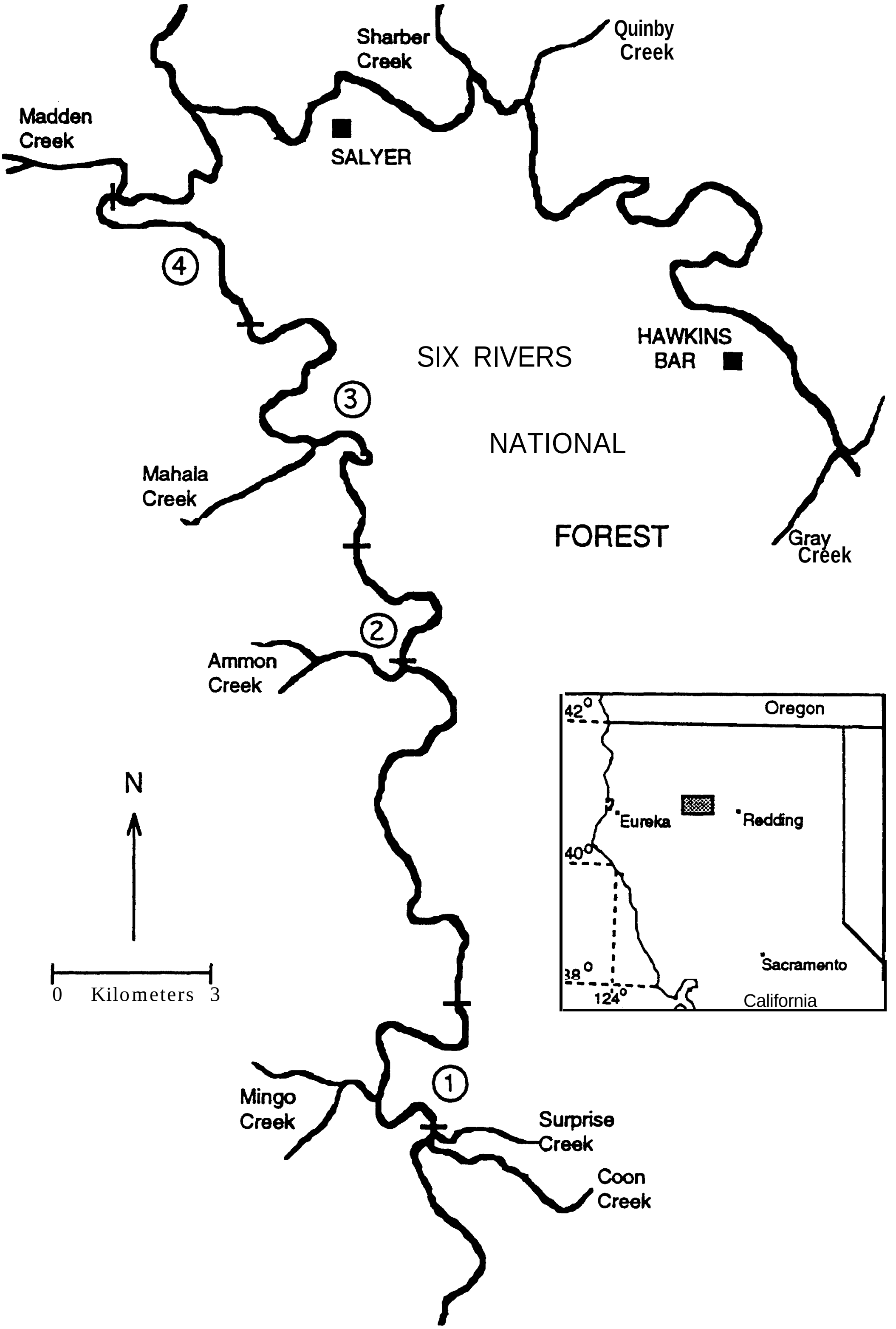

FIG. 2. Location of study reaches along the south fork Trinity River, Humboldt and Trinity Counties, California.

logistical constraints, reach 2 was only sampled during 1992 and 1994, yielding a total of seven rounds of capture. All captures occurred from April-September, before and after which western pond turtles are inaccessible due to overwintering (Reese and Welsh, 1997). The south fork sampling period started later (May) because high gradient rapids in the study area rendered it unswimmable until that time.

About one half reach was sampled per day (about 1.5 km), such that it took six to eight days to complete each round of capture at each study site. Sampling consisted of searching all swimmable areas within 4 m of the shoreline (see Reese, 1996) with the exception of steep reaches with swiftly flowing, turbulent waters (high gradient riffles: McCain et al., 1990). Juveniles (turtles <125 mm carapace length [CL]) were defined on the basis of CL using the known relationship between size and sexual maturity (D. Holland, pers. comm.). Existing evidence indicates that hatchlings and first year juveniles (<60 mm CL) inhabit specific microhabitats not used by the larger size classes (Holland and Bury, 1998) and not easily accessed by snorklers. Measures adopted to increase the probability of finding small turtles included visual searches of all inundated gravel bars and other areas too shallow to swim as well as searches of seasonal pools connected to the river. Special attention was given to root masses, emergent vegetation, and other fine-scale aquatic cover.

We used a standardized system for handling and marking previously applied to western pond turtles (Bury, 1972). The maximum carapace length in milimeters of each individual was measured using calipers with the long axis parallel to the plastron. Sex of adults was determined using a set of characteristics described by Holland and Bury (1998), which include carapace shape, plastron concavity, beak orientation, and head coloration. Each individual received a unique mark the following methods of Cagle (1939) and Ferner (1979).

Float Surveys.-Logistical limitations did not permit snorkeling of the remaining 13 reaches of the mainstem Trinity River study site (Fig. 1). However, "float surveys" were conducted, which consisted of two observers equipped with binoculars floating downstream on clear, sunny days between 0900 and 1730 hours and counting the number of basking turtles on both sides of the river. Observers floated four reaches per day such that it took four days to complete all 63 km of reaches. Surveys were conducted during July 1991, August 1991, May 1992, July 1992, and September 1992. Because reaches 10 and 11 played such a significant role in our calculations of population size for the whole study area (see data analysis), they were sampled multiple times during each sampling month and the counts averaged. In addition, each mainstem study reach was floated three times during July 1992 to obtain estimates of the sampling error.

Mark-Recapture Reaches.-Open population models, based on the Jolly-Seber model (Jolly, 1965; Seber, 1965) were used because they allow for birth, death, immigration, and emigration, all of which were likely to have occurred during the three-year sampling period. Survival parameters are reported, but given the ecology of the study species, we were unable to distinguish between deaths and emigration or between births and immigration. Western pond turtles leave the Trinity River for temporary terrestrial excursions (Reese and Welsh, 1997), and make long-distance aquatic movements (Holland and Bury, 1998), either of which could make these individuals effectively invisible in the mark-recapture samples for extended periods of time.

Each capture round was treated as a separate sample, such that there were nine total samples, and eight sampling intervals, for each study site. Overwintering periods were included in the sampling intervals because, although the turtles are dormant (Reese and Welsh, 1997), mortality may occur during that time. Reaches 10 and 11 of the mainstem and reaches 1, 3, and 4 of the south fork were each treated as single data sets, while separate models were applied to reach 3 of the mainstem and reach 2 of the south fork because they experienced fewer capture rounds.

The program RELEASE, which implements the method of Burnham et al. (1987), was used to determine whether each set of mark-recapture data fit the Jolly-Seber model. Fisher exact tests were used in the case of small cell counts. The JOLLYAGE program (Hines, 1990), implementing the models of Pollock (1981), was used to test whether survival and capture rates were different between age classes using contingency table chi-squares. For populations of aquatic turtles, survival rates are generally lower in the younger age classes because of their susceptibility to predation and abiotic factors (Iverson, 1991). There are also likely to be age-related differences in capture probability because the smaller body size and more cryptic habits of juveniles render them more difficult to capture (Congdon et al., 1993). If the JOLLYAGE tests yielded a statistically insignificant result, the two age classes were combined and the mark-recapture data were analyzed using the program JOLLY (Hines, 1990).

Both the JOLLY and JOLLYAGE models assume that: (1) marks are retained during the course of the study (2) captured individuals are released immediately after sampling (3) individuals have equal capture probabilities in each sample and (4) marked individuals have equal probabilities of survival to the next sampling period, with the exception of the variance between age classes allowed in JOLLYAGE. The first two assumptions were satisfied by the fact that individuals were released immediately after capture and marking, and all carapace notches were retained during the course of the study. Unequal capture probabilities can result either from trap-shy responses or heterogeneity in capture probability among individuals. If snorkellers consistently and thoroughly search turtle refugia, the effect of "snorkel-shy" responses on capture probabilities should be negligible. The chi-square tests identified whether individuals otherwise differed in their likelihood of being captured. There were not likely to be differences in survival rates between marked and unmarked individuals because the handling and marking techniques were noninvasive, and marks were cryptic with respect to predators. However, other heterogeneity in survival rates may have existed. Pollock et al. (1990) proposed that, in natural populations, for the common case of heterogeneous survival rates that are positively correlated for the same individual, biases on population size estimators are likely to be small.

Remaining Mainstem Reaches .-Using the population size estimates for mark-recapture reaches 10 and 11 generated from the mark-recapture data, we derived a ratio of basking turtles to resident turtles for these two reaches. A separate ratio was derived for each of the five sampling periods and a mean ratio then obtained. The results from reach 3 were not included in these calculations because the small number of captured turtles there seemed likely to bias the ratio. The ratio of baskers/ residents (reaches 10 and 11) was then applied to counts of baskers in the remaining 13 river reaches to derive estimates of residents (i.e., population size) for each sampling period. An overall estimate for the entire 63 km stretch of river was obtained by adding the model-generated population estimate for reaches 10 and 11 to the mean population size across sampling periods for the other reaches. A standard deviation was calculated for the population estimate for each sampling period by incorporating the error in the denominator yielded by the Jolly-Seber model as well as the numerator error representing variability in counts of basking turtles. The error term for the overall population estimate incorporated the error from each sampling period.

Population Density.-Population densities were calculated by dividing the population estimates by an estimate of river surface area for each study site. Calculation of densities was restricted to those reaches for which we had Jolly-Seber population estimates (mainstem reaches 10 and 11, south fork reaches 1,3, and 4). The river surface areas of mainstem reaches were obtained from a geographical information system (GIS) map of the river contour created from aerial photographs (R. A. Wilson, unpubl. data). River surface areas of south fork reaches were obtained from a GIS map of the river contour that was created by digitizing the right and left banks from a topographic map. Densities of turtles at the two study sites were compared using a two-tailed approximately normal test of equality (B. Noon, pers. comm.; Pollock et al., 1990).

Population Structure.-Because this study lacked the longevity and high juvenile capture rate required for growth rate information, we selected a more conservative method of comparing population structure, specifically to group individuals into just two size/ age classes. Mean tallies of adults and juveniles across years were then calculated to obtain an estimate of average age structure for each site. Average age structure was also derived from nine years of data (1987-1995) from Hayfork Creek, a tributary of the south fork Trinity (Holland and Bury, unpubl.). Hayfork Creek has a stable size/ age distribution relative to 1968-1972 censuses (Bury 1972; D. Holland, pers. comm.), thus it served as a useful comparison to the Trinity populations. Chi-square contingency table analysis was used to assess whether the proportion of juveniles and adults differed among the three populations. Multiple comparison proportion tests (Zar, 1984) identified which pairs of proportions were responsible for the difference.

RESULTS

Poplation Size

Mark-Recapture Reaches.-For the larger mainstem data set (reaches 10 and 11), the results of JOLLYAGE provided evidence for an age-dependent effect (overall chi-square = 7.79, 1 df, P = 0.0053); the recapture probability for juveniles was lower than that for adults. Model A2 (the standard Jolly-Seber with age-dependency) best fit the data; the contingency chi-square table was nonsignificant, indicating no lack of fit to the model (overall chi-square = 11.86, 9 df, P = 0.22). However, because of low sample sizes of captured juveniles, survival rates for the juvenile age class were not estimable for most sampling periods, and estimates of recruitment (birth plus immigration) were confounded. For the smaller datasets (mainstem reach 3 and southfork reach 2), the effects of small sample size were even more apparent; there were not enough data to perform the JOLLYAGE tests of age-dependence. We abandoned the age-dependent models altogether, deeming them too complex for the data.

TABLE 1. Jolly-Seber estimates and approximate standard errors under the Jolly-Seber model (A) for western pond turtles in the mainstem Trinity River, reaches 10 and 11, captured during nine sampling periods from 1991-1993. N_i = population size. o_i = survival rate per unit time.

Sampling period	Date	N_i	SE	o_i	SE
1	June 1991	—	—	1.00	0.005
2	July 1991	590	260.4	1.00	0.001
3	April 1992	180	40.1	1.00	0.006
4	May-June 1992	216	47.6	1.00	0.006
5	July 1992	179	44.0	1.00	0.011
6	August 1992	230	70.0	1.00	0.023
7	September 1992	207	129.9	1.00	0.002
8	May 1993	185	55.0	—	—
	$\bar{x}$	255	45.2	1.00	0.003

TABLE 2. Jolly-Seber estimates and approximate standard errors under the death but no immigration model (A') for western pond turtles in reach 3 of the mainstem Trinity River captured during seven sampling periods from 1992-1993. [a] Not estimable due to insufficient data for this model.

Sampling period	Date	N_j	SE
1	April 1992	28	0.0
2	May-June 1992	63	35.5
3	July 1992	44	18.5
4	August 1992	77	NE[a]
5	September 1992	20	9.9
6	May 1993	8	NE
	$\bar{x}$	40	NE[a]

A total of 247 unique (i.e., first-capture) turtles were caught on mainstem reaches 10 and 11 during the course of the study. For these reaches, the chi-square contingency table tests in RELEASE indicated no reason to reject the Jolly-Seber model (overall chi-square = 17.85, 28 df, P = 0.93). Both model A (standard Jolly-Seber) and model B (constant-survival) fit the data, whereas the goodness-of-fit tests produced significantly larger chi-square values for models A' and D (Reese, 1996). The test comparing model A to model B did not reject the simpler model (B) in favor of A chi-square = 3.68, 6 df, P = 0.72). However, examination of the parameter estimates revealed greater precision from model A (Reese, 1996); the standard errors for the population size estimate and the survival estimate were smaller. Indeed, Pollock et al. (1990) noted that when estimating the average population size across sampling periods, an average of the Jolly-Seber estimates N_i may be more precise than an average of the model B or D estimates. Pollock et al. (1990) attributed this precision to the fact that in these simpler models the N_i estimators tend to be positively correlated with one another. We, therefore, report the mean population size estimate across all sampling periods for these reaches to be 255 individuals with a standard error of 45 (Table 1).

A total of 34 unique turtles were caught on mainstem reach 3. Only two sampling periods had sufficient data for calculation of the goodness-of-fit test in RELEASE. However, overall test results indicated no evidence for lack of fit to the Jolly-Seber model (overall chi-square = 1.32, 13 df, P = 0.72). Model A' (no immigration) fit the data best (overall chi-square = 1.06, 2 df, P = 0.59) and provided a population estimate of 40 individuals for this reach. Standard errors were not generated, nor were survival rates estimated because of the small sample size (Table 2).

A total of 230 unique turtles were caught on south fork reaches 1, 3, and 4. RELEASE indicated no reason to reject the Jolly-Seber model (overall chi-square = 25.5, 19 df, P = 0.14). Of the models examined, models A, A', and D all fit the data (Reese, 1996). The goodness-of-fit tests revealed no significant difference between the fits for model A (standard Jolly-Seber) and the two simpler models. Examination of the model A estimates revealed that standard errors were not estimable for some parameters during some sampling periods, indicating insufficient data for this model (Reese, 1996). Comparison of the remaining models indicated higher precision for model A' (Reese, 1996); it yielded smaller standard errors for both the population size and the survival estimate (Table 3). We thus selected model A' (death, but no immigration) as the most suitable, yielding a mean population estimate of 447 (SE = 118, Table 3).

A total of 48 unique turtles were captured on reach 2 of the south fork. RELEASE indicated no lack of fit to the Jolly-Seber model (overall chi-square = 6.24, 10 df, P = 0.79), although two sampling periods had insufficient data due to few captures. Model A' appeared to best fit the data (overall &-square = 0.495, 2 df, P = 0.78) and provided a population estimate of 53 individuals for this reach (standard error = 12; Table 4). Survival rates were not estimated as a result of the small sample size.

Examination of the capture histories for both study sites revealed an unusual pattern in the data. In reaches 10 and 11 from the mainstem site, numerous individuals captured in the first few sampling periods were not recaptured until the last few sampling periods (Table 5). For example, eight individuals captured in period 2

TABLE 3. Jolly-Seber estimates and approximate standard errors under the death but no immigration model (A′) for western pond turtles in reaches 1, 3, and 4 of the south fork Trinity River captured during nine sampling periods from 1992–1994.

Sampling period	Date		N_i	SE		SE
1	July 1992		388	84.7	1.00	0.009
2	Early August 1992		335	69.3	1.01	0.028
3	Late August 1992		407	132.6	1.04	0.049
4	September 1992		979	918.8	1.00	0.003
5	June-July 1993		454	84.1	1.00	0.004
6	September 1993		433	86.2	1.00	0.001
7	June 1994		330	77.4	1.00	0.014
8	July 1994		247	94.4	—	—
		$\bar{x}$	447	118.5	1.00	**0.007**

were not recaptured until period 8 (two years later). This difference is in contrast to the more common pattern of individuals being recaptured soon after their first capture and then not recaptured at all.

At both study sites, capturing western pond turtles proved challenging because these cryptic reptiles utilized a variety of underwater refugia, some of which were difficult to search. Refugia included undercut banks and mammal (e.g., river otter) caves, beaver dams and other piles of woody debris, sand and silt, large boulders, and root masses. Mean capture probability (across all sampling periods) was 15.3% for turtles on the mainstem and 9.2% for turtles captured on the south fork.

Remaining Mainstem Reaches.-The ratio of basking turtles to resident turtles on reaches 10 and 11, derived from the mark-recapture data, ranged from 2.0% to 20.8% (Table 6). With the exception of the September 1992 sample, the ratios are relatively consistent. The low ratio during this late sampling period (resulting from only four turtles observed basking) can be attributed to a seasonal effect. Radiotelemetry data (Reese and Welsh, 1997) indicated that by September, turtles are leaving the river to travel to terrestrial overwintering sites. It is likely that during this survey only a small fraction of the population still resided in the river. Because such low counts are likely to bias the population estimates, this survey was excluded from the analysis.

Population estimates for all 16 study reaches including the "gap" reaches (Fig. 1) ranged from a total of 1145 to 1544 turtles (Table 6) with standard deviations ranging from 135 to **175.** Averaging across all sampling periods, an estimated 1210 western pond turtles inhabit the 63-km stretch of river between the Lewiston Dam and the confluence with the north fork Trinity.

Population Density

Analysis of polygons from the subdivided river contour revealed that mainstem reaches 10 and 11 total 13.27 ha in size, yielding a density estimate of approximately 19 turtles/ ha. The

TABLE 4. Jolly-Seber estimates and approximate standard errors under the death but no immigration model (A') for western pond turtles in reach 2 of the south fork Trinity River captured during seven sampling periods from 1992-1994.

Sampling period	Date		N_i	SE
1	July 1992		43	2.1
2	Early Aug 1992		65	26.8
3	Late Aug 1992		59	30.9
4	September 1992		54	19.3
5	June 1994		32	22.1
6	July 1994		66	56.9
		$\bar{x}$	53	12.3

TABLE 5. Summary table of capture histories for western pond turtles caught on the mainstem Trinity River during nine sampling periods from 1991–1993.[a]
[a] B-Table format from Leslie et a1.1953. [b] See Table 2 for dates of sampling periods.

Time of last capture (sampling period)[b]	Time of recapture (sampling period)[b]								
	1	2	3	4	5	6	7	8	9
1	0	5	5	1	0	1	0	2	2
2	0	0	10	12	7	6	2	8	5
3	0	0	0	6	5	3	2	3	1
4	0	0	0	0	6	1	2	6	4
5	0	0	0	0	0	2	4	4	2
6	0	0	0	0	0	0	2	5	3
7	0	0	0	0	0	0	0	1	1
8	0	0	0	0	0	0	0	0	9
9	0	0	0	0	0	0	0	0	0

TABLE 6. Estimates of western pond turtle population size and standard deviations derived from counts of basking turtles along 16 study reaches (63 km) of the mainstem Trinity River, California. [a] Not computed due to low sample size of basking turtles.

Sampling period	Ratio of Baskers/ Residents (reaches 10 and 11)	Population size (all 16 reaches)	
		Mean	SD
July 1991	41/255 = 16.1%	1544	169 individuals
August 1991	53/255 = 20.8%	1145	135 individuals
May 1992	51/255 = 23.0%	1240	149 individuals
July 1992	47/255 = 18.4%	1416	175 individuals
September 1992	5/255 = 2%		0[a]
$\bar{x}$	48/255 = 18.8%	1210	79

south fork reaches 1, 3, and 4 total 34.45 ha in size, yielding a density estimate of 13 turtles/ha. The mainstem density was not significantly different from that of the south fork (two tailed test; Z = 0.08, $P = 0.92$).

Population Structure

Size structure histograms for the mainstem Trinity, south fork Trinity, and Hayfork Creek populations display a difference in the proportion of juveniles to adults (chi-square = 6.1, $P < 0.05$; Fig. 3). Proportion tests indicated that the mainstem Trinity has a significantly smaller proportion of juvenile turtles than Hayfork (q = 3.87, $P < 0.05$). The size/age structures were not significantly different between the south fork and the mainstem (q = 2.47, $P > 0.05$) or the south fork and Hayfork (q = 1.62, $P > 0.05$). Examination of the JOLLYAGE results indicates that juvenile turtles at the mainstem site have significantly lower recapture probabilities than adult turtles (&-square = 7.79, $P = 0.0053$). While 39% of captured adult turtles were eventually recaptured, only 15% of juveniles were recaptured. At the south fork site, in contrast, the recapture probabilities were not significantly different (chi-square = 4.93, $P = 0.1768$). Twenty-five percent of adults and 23% of juveniles were eventually recaptured. Proportion tests (Zar, 1984) revealed that mainstem adult turtles have a significantly higher recapture probability than south fork adults (q = 4.89, $P < 0.05$), while juveniles do not differ in capturability between the two sites (q = 1.16, $P > 0.05$).

DISCUSSION

The unusual capture histories for both the mainstem and the south fork populations suggest that some form of temporary emigration may have occurred during the study. Some turtles are effectively "disappearing" from the population between their first capture and subsequent captures, whether it be actual departure from the study area or departure from the capturable population (e.g., turtles moving into inaccessible underwater refugia). This pattern has been observed at other long-term study sites for western pond turtles; it is not uncommon to have 1-2 years between captures even if an area is intensively sampled (D. Holland, pers.

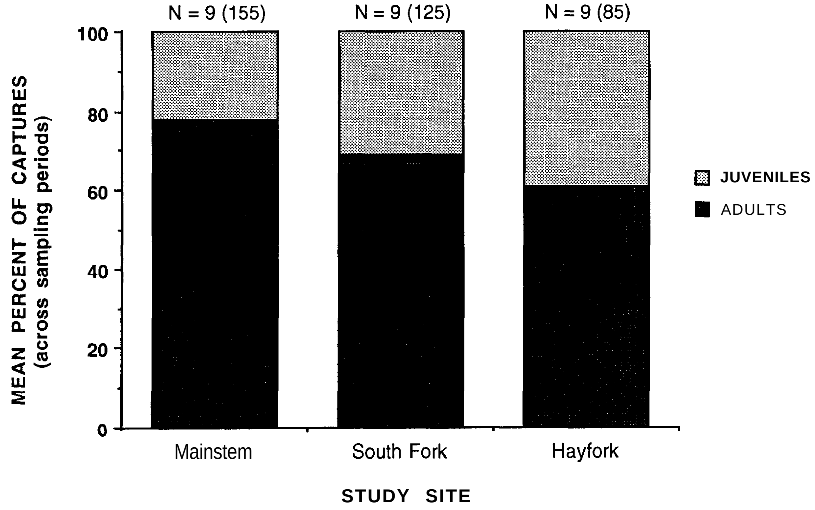

FIG. 3. Percent of captured turtles that were adults and juveniles at each of three sites in the Trinity River System, California. Percents are averaged across sampling periods for each site. N = number of sampling periods (n = number of captures). Hayfork Creek data are from Bury and Holland (unpubl.).

comm.). Results of the goodness-of-fit tests in the JOLLY program do not provide evidence that the temporary emigration is Markovian (i.e., related to previous locations; J. Nichols, pers. comm.), suggesting that the unusual capture histories stem from random temporary emigration or low capture probabilities or both. Temporary emigration certainly does occur, both within the watercourse and onto land, as evidenced by our radiotelemetry results (Reese and Welsh, 1997). Low capture probabilities also occur because western pond turtles are cryptic and able to access effective refugia. While Markovian temporary emigration leads to biased estimates of population size, random temporary emigration does not (J. Nichols, pers. comm.).

The densities of western pond turtles in both the mainstem and the south fork of the Trinity River were low, considering that this species achieves densities as high as 1000 individuals/ha at other locales (Holland and Bury, 1998). The density in nearby Hayfork Creek has been as high as 445 individuals/ ha (Bury, 1972). The low density in the mainstem is likely not attributable to the dam, since densities in the free-flowing south fork are not significantly different. Low densities may result from characteristics of these sites with respect to resource distribution. They are both large rivers with food, cover, and basking site resources restricted to the shorelines (Reese and Welsh, 1998), such that density estimates may be deflated by much of the middle river area consisting of unsuitable habitat. Other large rivers in the Pacific Northwest contain similar low densities of western pond turtles with an inverse relationship appearing between stream order and density of western pond turtles (D. Holland, pers. comm.). Evidence suggests that primary production and other carbon inputs decrease as stream size increases within a certain range (e.g., Naiman, 1987), which may limit food availability to turtle populations inhabiting large rivers. Alternatively, impacts on both the mainstem and south fork of the Trinity River may have depressed the size of western pond turtle populations. The mainstem has been dramatically altered by mining, logging, and damming (USDI Bureau of Land Management, unpubl. data), and the south fork has experienced substantial logging (USDA Forest Service, unpubl. data), although Hayfork Creek has also been impacted by mining and logging (Bury, 1972). Further research on range wide population densities might clarify the significance of the low densities in the Trinity system.

The results of the size/ age structure analysis indicated that the mainstem population has a smaller proportion of juveniles than the Hayfork population, which is known to have been stable during a 25-year period. This difference could result from lower recruitment of juveniles into the population, lower survival rates of juveniles, or a bias from lower capture rates of juveniles in the mainstem, or some combination of these factors. There is evidence from the JOLLYAGE results that survival or recapture probabilities, or both, for juveniles were lower than those for adults in the mainstem. However, the JOLLYAGE tests do not distinguish lower survival probabilities from lower capture probabilities, since these effects have the same outcome in the sampled population. Lower capture probabilities could result from the fact that juveniles are primarily captured by visual location and water clarity is often poor on the mainstem Trinity (D. Reese, pers. obs.). The factors potentially causing lower survival rates require further investigation. The smaller body size of juveniles poses an increased susceptibility to predation from aquatic predators such as river otters *(Lutra canadensis)* and minks *(Mustela vison)*. Changes wrought by the dams, including a decrease in shallow edgewaters, and a lowering of water temperatures (Hampton, 1995), could also impact juvenile turtles, which are associated with lentic, warm waters (Reese, 1996; Holland and Bury, 1998).

The combination of low densities and an adult-dominated age structure on the mainstem Trinity River is not indicative of "healthy" populations. Because of its size and gradient, the Trinity River may never have been a highly productive area for western pond turtles. The San Joaquin Valley (Tulare Lake, Kern Lake, and Buena Vista Lake) is known to have harbored extremely dense populations prior to large-scale agricultural development (Preston, 1981; Holland and Bury, 1998). Habitat provided by the historic, huge, shallow lakes certainly contrasts with the small pockets of lentic water currently available in the Trinity River. Higher-order streams such as the Trinity may play a supplementary role in the ecology of the species, serving as corridors for migration and gene exchange between slower streams and adjacent ponds. Indeed, at both the mainstem and south fork sites, turtles make seasonal journeys to other bodies of water (Reese and Welsh, 1997). Habitat provided by the Trinity River system may take on increased significance now that western pond turtle habitat in other locations, such as the San Joaquin and Sacramento Valleys, has been altered and eliminated.

Western pond turtles typify the order Testudines in having long life spans, delayed sexual maturity, iteroparity, and high adult survival rates (see Wilbur and Morin, 1988). This characteristic suite of life history traits results in turtle populations that are limited in their ability to rebound from increased mortality of any age class. Despite high adult survivorship, low fecundity and low nest survival necessitate extremely high juvenile survival to maintain stable populations (Congdon et al., 1993). In general, species with low intrinsic rates of increase face higher extinction probabilities because their populations recover slowly from a depressed condition (Pimm et al., 1988). Long-lived species also show a lag time in their response to population impacts because of long generation times and consequently slow replacement rates even under natural conditions. Thus, particular attention should be paid to evidence of skewed age structures or other indications of population sinks because they indicate long-term impacts to populations with limited recovery capabilities.

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