

Columbia River Project Water Use Plan

KINBASKET AND ARROW LAKES RESERVOIRS

Supplemental Report

Reference: CLBMON-37

Amphibian and Reptile Life History and Habitat Use Assessment: Western Painted Turtle Population Trends Assessment

Study Period: 2010-2017

LGL Limited environmental research associates, Sidney, BC
Okanagan Nation Alliance, Westbank, BC

August 2021

Note to Reader

There is broad agreement that leading stressors to the Western Painted Turtle population considered in this report are unrelated to BC Hydro's operations (Basaraba 2014, Duncan 2016, current report). BC Hydro has met all requirements Ordered under our Columbia Water Licence with relevance to Western Painted Turtle. The report that follows was commissioned by BC Hydro to re-assess population size – a goal identified under Ordered work (CLBMON-37), leveraging data made available under a different project. Assessing a temporal trend in population size was peripheral to the Ordered work and was therefore a secondary objective that was conditional on the suitability of the data, given analysis requirements.

BC Hydro maintains that pre-existing science provided rationale that the data were not suitable for the type of analysis performed. BC Hydro is aware that the results of the trend analysis could be meaningful to other agencies concerned with the status and management of intermountain Western Painted Turtle. For transparency, all parties agreed to publishing the analysis with the inclusion of this note to disclose BC Hydro's concerns.

BC Hydro observed that the strong result – a population decline of 29.3% over eight years – was unrelated to the number of individuals captured each year; nor was the result explained by changes in age-distributions over time (data available in Table 1 and Appendix A). The only feature of the data consistent with the result was a striking under-representation of smaller turtles in the analyzed data (Figure 3).

In a stable population, younger cohorts should be more numerous than older cohorts. A population with an age-profile as shown in Figure 3 clearly has insufficient recruitment and is in a phase of decline; however, it was unclear if the observed age distribution represents the population's age-structure, or a selective capture process. The model had the capacity to infer a population trend based on the observed age-structure, which was why equal-catchability among age cohorts was an essential condition of analysis. However, probability of turtle capture is known to be strongly influenced by their size/age (Gamble 2006, Pike et al. 2008, Tesche 2014, Tesche and Hodges 2015, Gulette et al. 2019), and unequal capture is pervasive in adult cohorts (Koper and Brooks 1998). The scientific community has previously warned against analytical interpretations based on the size of captured turtles (Tesche and Hodges 2015). The shape of the relationship between capture probability and turtle size remains unclear, and the use of a minimum size threshold to control for capture bias is speculative.

BC Hydro was concerned that despite controls applied, larger adult turtles were still easier to catch than smaller adult turtles and saw no evidence to suggest that capture bias above the minimum threshold size (120 mm) was not strongly influential to the result. It remained unclear to what degree the trend detected was an artefact of capture bias, making interpretation problematic.

BC Hydro recommends that this outstanding issue is further assessed and considered by readers.

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KINBASKET AND ARROW LAKES RESERVOIRS

Monitoring Program No. CLBMON-37

Kinbasket and Arrow Lakes Reservoirs: Amphibian and Reptile Life History and Habitat Use Assessment



Western Painted Turtle Population Trends Assessment Final Report 2017

Prepared for



BC Hydro Generation

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From left to right: Hatchling Western Painted Turtles ("scooters"), Female Western Painted Turtle digging nest at Red Devil Hill; Juvenile Western Painted Turtle with transmitter; Juvenile Western Painted Turtle habitat at Airport Marsh. Photos © Jenna Boisvert, Okanagan Nation Alliance, Jessica Zahnd, and Virgil C. Hawkes, LGL Limited environmental research associates.

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Executive Summary

The Western Painted Turtle (*Chrysemys picta bellii*) population at Revelstoke Reach in Arrow Lakes Reservoir has been studied since 2010. The results of previous work have provided some insight regarding the occurrence and distribution of turtles, general habitat use, and over-winter behaviour. However, questions remain regarding the utility of the existing data to estimate population size and assess annual variation in population size. We used an integrated age-structured mark-recapture model to answer questions regarding the abundance and associated population trends of the Western Painted Turtle population in Revelstoke Reach of Arrow Lakes Reservoir. This work was completed to address management question 2 of the CLBMON-37 scope of services as it relates to the Western Painted Turtle population.

The integrated age-structured mark-recapture model combines attributes of a traditional Jolly-Seber mark-recapture model with virtual population analysis (VPA) methods widely used in fisheries stock assessments into a single analysis framework. The model operates in discrete time, creating a virtual reconstruction of sex-specific abundances across age and time that best matches observed captures within the assessment period (i.e., 2010-2017). Unknown parameters include the number of individuals entering the population, both historically and within the assessment period, mortality-at-age rates and yearly sampling rates (used to derive capture probabilities). Unknown parameters are estimated by minimizing the discrepancy between observed and predicted catches over age, time, and sex, with predictions generated from the VPA portion of the model. The integration of two separate analysis approaches into a single analysis framework also provides the ability provide estimates of uncertainty on future population projections. Furthermore, these types of integrated population models have been shown in practice to provide to more robust and precise estimates of abundance relative to classical abundance estimation techniques.

Results from the analysis suggest that the adult Western Painted Turtle population in Revelstoke Reach may have undergone a statistically significant decline since 2010. Total adult abundance (i.e., age 10+) was estimated at approximately 890 adult turtles in 2010, declining to roughly 630 adults by 2017. The average yearly change in the number of adults (i.e., change in the number of turtles per year) was used to quantify the population trends, estimates suggesting a loss of approximately 36 turtles per year (95% Credible Interval [CI]: -49.7, -24.9 turtles per year). The decline also appeared affect both sexes similarly (95% CI – females: -24.3, -8.6 turtles per year; males: -28.9, -13.5 turtles per year). Comparing the population size at the start and end of the study period indicated an estimated 29.3% decline in the total population (95% CI: -39%, -19%) with similar levels of decline exhibited by both sexes (95% CI – females: -38.0%, -15.3%; males: -41.6%, -19.6%). The coefficient of variation in this trend estimate was about 17 to 20 per cent; however, the estimated trend was larger than five standard deviations away from the mean.

The current analysis attempted to model Western Painted Turtle population dynamics; however, turtle aging and the observed age structure in the sample were two of the main limitations encountered with this analysis. The input data were limited to adult captures only, due to lower capture rates associated with smaller younger individuals. Because the model was age structured, and a size-selectivity curve could not be estimated as part of the analysis model, an assumption that the age structure of sampled adults accurately reflected the true adult age structure of the population was required; an assumption that could not be directly assessed. If older adults were caught at significantly higher rate than younger adults, this could have exacerbated trend estimates. However, if the probability of capturing an adult turtle, regardless of size, was similar for all age (and size) classes, the results as presented may be plausible. The lack of available sex-specific growth rates meant that turtles ages were approximated, based on best available



information. While this should have a minimal effect on the estimate of adult abundances (i.e., only adults were considered in the analysis), the temporal accuracy of recruitment estimates could have been affected. Additional limitations in the analysis include different capture probabilities associated with notched vs. notched with radio transmitter may have affect estimates of detection, and in turn, the scaling of the estimated population size. However, this limitation was considered to be minor as sensitivity analyses demonstrated that the estimated trends were consistent across methodology-related data subsets (e.g., all data, notched only, notch with radio transmitter only, and 2014 to 2016 data only). This suggests the estimated trends are largely insensitive to differences in data generated by these alternate methods. Finally, the model did not consider the spatial distribution of turtles; spatially aware models could further refine estimates and understanding of population dynamics.

The analysis undertaken cannot speak to causation of populations trends. However, following roughly 10 years of study, there are several possible factors that might be influencing the turtle population in Revelstoke Reach. These include road-based mortality of females during the nesting period, reduced habitat suitability at nesting sites (which occur outside of the drawdown zone), nest predation, and increased (although unmeasured) rates of predation on juveniles. Each of these factors could contribute directly and indirectly to the estimated trends reported herein. Previously completed work indicated that the turtle populations in Revelstoke Reach will experience potential, seasonal (and temporary) habitat displacement relative to changing reservoir levels but the overall impact of reservoir operations on turtles appears to be negligible. Without consideration of all variables that influence recruitment, mortality, and survival there will continue to be a larger degree of uncertainty associated with population trend projections.

Keywords: Western Painted Turtle, virtual population analysis, reservoir, Arrow Lakes.



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Introduction and Background

The Columbia River Water Use Plan (WUP; BC Hydro 2007) was developed as a result of a multi-stakeholder consultative process to determine how to best operate BC Hydro's Mica, Revelstoke, and Keenleyside facilities to balance environmental values, recreation, power generation, culture/heritage, navigation, and flood control. The goal of the WUP is to accommodate these values through incremental changes to how water control facilities store and release water, or to undertake physical works in lieu of changes to reservoir operations to meet the specific interests. During the WUP, the Consultative Committee (CC) supported the implementation of physical works (revegetation and habitat enhancement) in the mid-Columbia River in lieu of changes to reservoir operations to help mitigate the impact of Arrow Lakes Reservoir operations on wildlife and wildlife habitat. In addition, the CC also recommended monitoring the effectiveness of these physical works at enhancing habitat for wildlife.

During the Columbia WUP, the Western Painted Turtle (*Chrysemys picta* pop. 2, Intermountain – Rocky Mountain population) was identified as a species that may be vulnerable to fluctuating water levels resulting from operations of the Arrow Lakes Reservoir. It is a provincially blue-listed species and the intermountain population is listed as Special Concern under Schedule 1 of SARA (COSEWIC 2006). The population that occurs near Revelstoke, BC is one of the most northern populations and has regional importance (Schiller and Larsen 2012a and 2012b; Maltby 2000). Furthermore, the Western Painted Turtle was identified as a species that may benefit from habitat enhancement via physical works (Golder Associates 2009a and 2009b).

Western Painted Turtles are small freshwater turtles with smooth, dark carapaces with pronounced red and yellow pigmentation on the limbs and plastron. They are slow to mature sexually (e.g., 5 to 6 years for males and 7 to 8 years for females; Ernst and Lovich 2009) and long-lived, living to 50 years or more. They are found in the shallow water ponds, lakes, sloughs, and slow-moving streams or rivers, but like many aquatic reptiles they require various habitats corresponding to their life history needs. These include: 1) summer habitat with muddy substrates, an abundance of emergent vegetation, and numerous basking sites; 2) nesting habitat with loose, warm, well-drained soils; and 3), aquatic overwintering habitat that does not freeze and does not become severely hypoxic (COSEWIC 2006). Western Painted Turtles mate underwater in warm shallow water in the spring and summer. Nesting sites are typically within 150 meters from pond margins and are composed of loose, warm, well-drained soils, often on south-facing slopes (COSEWIC 2006). Gravid females bury 6 to 22 eggs in a flask-shaped nest, which begin to hatch in late summer. Hatchlings remain dormant in the nest until the following spring.

Western Painted Turtles are found in all provinces in Canada except Prince Edward Island, Nova Scotia, New Brunswick and Quebec. The species range appears to be limited by the length of the turtle's active season, mean ambient temperature during egg incubation, and mean winter temperature (COSEWIC 2006). Given this species' low adult recruitment, delayed maturity, and high adult survival, chronic added mortality of juveniles and adults could eliminate local populations (COSEWIC 2006). Factors contributing to low survivorship include road mortality (particularly of gravid females during the nesting season), predation on dispersing turtles, and depredation of nests. Degradation of nest site suitability is also a threat (e.g., Western Painted Turtle Recovery Team 2016). While reservoirs have contributed to changes in Western Painted Turtle habitat suitability and fluctuating water levels have been linked to increased predation risk



(COSEWIC 2006), the impacts of reservoir operations on Western Painted Turtle populations remain poorly understood.

During 2010 and 2011, a Master of Science research project was conducted to collect baseline data on a population of Western Painted Turtles near Revelstoke, BC (Basaraba 2014). The goal of this study was to determine the extent to which painted turtles use the reservoir, provide a preliminary assessment of the population, assess potential impacts of reservoir operation in turtles, and develop a long-term monitoring strategy to address the concerns raised during the WUP. This two-year study used a number of techniques including visual encounter surveys (VES), nesting and hatchling emergence surveys, trapping, mark-recapture, and radio telemetry to obtain data on painted turtles. A monitoring strategy was developed by Schiller and Larsen (2012b) who identified key information gaps and outlined how to proceed to determine the impacts of reservoir operations on Western Painted Turtles in Arrow Lakes Reservoir near Revelstoke BC and address management questions and hypotheses. Monitoring continued through 2012 (Hawkes et al. 2013), 2013, and 2014, providing further insights on painted turtle productivity, habitat use, and overwintering preferences. An assessment of winter-habitat use was completed in 2014 (Duncan 2016). In 2015, the third component of this long-term study began, looking at juvenile survivorship and habitat use (Wood et al. 2016).

This report summarizes the results of age-structured mark-recapture model to estimate population size and assess annual variation in population size. The results of the analysis provided an estimate of the population trend, and population trajectory, along with estimates of uncertainty.

The management questions (MQ) associated with this monitoring program are listed below. Of the questions, question b is of relevance to this work.

- a. Which species of reptiles and amphibians occur within the drawdown zone and where do they occur?
- b. What is the abundance, diversity, and productivity (reproduction) of reptiles and amphibians utilizing the drawdown zone and how do these vary within and between years?
- c. During what portion of their life history (e.g., breeding, foraging, and overwintering) do reptiles and amphibians utilize the drawdown zone?
- d. Which habitats do reptiles and amphibians use in the drawdown zone and what are their characteristics (e.g., pond size, water depth, water quality, vegetation, elevation band)?
- e. How do reservoir operations influence or impact reptiles and amphibians directly (e.g., desiccation, inundation, predation) or indirectly through habitat changes?
- f. Can minor adjustments be made to reservoir operations to minimize the impact on reptiles and amphibians?
- g. Can physical works projects be designed to mitigate adverse impacts on reptiles and amphibians resulting from reservoir operations?
- h. Does re-vegetating the drawdown zone affect the availability and use of habitat by reptiles and amphibians?
- i. Do physical works projects implemented during the course of this monitoring program increase reptile or amphibian abundance, diversity, or productivity?
- j. Do increased reservoir levels in Kinbasket Reservoir during the summer months resulting from the installation of Mica 5 and 6 negatively impact amphibian populations in the drawdown zone through increased larval mortality or delayed development?



Scope of Work

The key objective of this work is to address Management Question b (above; MQ-2 in other references) specifically for the Western Painted Turtle for which there is special concern due to its current conservation designation (Provincially blue-listed, COSEWIC Species of Special Concern [2016] and SARA, Schedule 1 species of Special Concern [2007]) and due to the regional significance of the Revelstoke population. Furthermore, radio-telemetry data collected on the Revelstoke population of Western Painted Turtle (conducted under CLBMON-11B3) present a unique opportunity for addressing this management question to a higher level than would normally be possible under work typically associated with CLBMON-37. These data have not previously been applied to answering management question b with respect to Western Painted Turtle. The results of this modelling exercise will answer the following questions in order of priority:

1. What is the estimated size of the Western Painted Turtle population? Does it vary by sex?
2. Is the population increasing, decreasing, or stable? Does the trend vary by sex?
3. What are the yearly recruitment rates? Does recruitment vary by sex and/or over time?
4. What are the age-specific survival rates? Does survival vary by sex or over time?
5. Based on questions 1) to 3), what is the estimated size of the turtle population in 5, 10, 20, and 40 years? Is the outlook different for each sex?

Methods

Definitions

Several terms are defined below to ensure proper interpretation.

Term	Definition
Freely Estimated	Parameter value was not constrained by a function of other parameters or data.
Prior distribution	A prior probability distribution expresses one's knowledge about the value of an unknown model parameter before further evidence is taken into account.
Hyperprior	A hyperprior is a prior distribution on a hyperparameter, that is, on a parameter of a prior distribution.
Informative Prior	An informative prior expresses specific, definite information about a parameter within a Bayesian statistical model.
Uninformative Priors	An uninformative prior or diffuse prior expresses vague or general information about a parameter within a Bayesian statistical model.
Posterior Sample	The posterior sample is a probability sample drawn by the Markov chain Monte Carlo algorithm from the posterior distribution for an unknown model parameter. The posterior distribution summarizes the knowledge about the unknown parameter value, conditional on the evidence obtained from a study. "Posterior", in this context, means after the relevant evidence related study has been collected.
Posterior Predictive Distribution	The posterior predictive distribution is the distribution of possible unobserved model parameter values (e.g., abundance in a given age class) conditional on the observed values. Predictions include all sources of uncertainty including uncertainty in dependent parameter values.



Empirical Data and Model Inputs

The Western Painted Turtle population in Revelstoke Reach has been studied since 2010; a summary of methods, including capture and trapping methods can be found in Wood et al. (2016). Between 2010 and 2016, 407 individuals have been captured and 324 of those marked. Marking included notching [(Cagle (1939) as recommended by RISC (1998))] or notching plus the application of a VHF radio-transmitter. From these data, we extracted a sample of 230 adult turtles (n=92 males and n=138 females) that were marked (either with notching [n=125] or notching and a transmitter [n=76]) and measured. Adult turtles can achieve a straight-line carapace length of 266 mm (Marchand et al. 2015). Male and female Western Painted Turtles reportedly mature at different sizes and ages: males: 70 to 95mm; 2 to 4 years; females 97 to 128 mm; 6 to 10 years (Ernst and Lovich 2009). For this work, turtles with a straight-line carapace length >120 mm were assigned to the adult age class for both males (120 mm to 189mm) and females (120 mm to 220 mm; Appendix A: Capture Data). Of the 230 turtles, 201 were associated with carapace measurements (n=91 males and n=110 females). This final subset of the marked population was used in the modelling exercise (Appendix A: Capture Data). Notched turtles were recaptured 1.2 times on average, while turtles with notching and a transmitter were captured 1.6 times on average over the course of the study.

Yearly sampling was conducted by different groups including graduate students (Basaraba; Duncan) and LGL/ONA biologists. The data collected during each year of study was collected for purposes ranging from assessing the effects of reservoir operations on turtles (Basaraba 2014), studying overwintering ecology of turtles (Duncan 2016), and to fulfill requirements under CLBMON-11B3 and CLBMON-37. As a result, the sampling effort varied annually and was not consistently documented in all years (Table 1), requiring sampling rates to be freely estimated for each year of study (see Population Model). Furthermore, year-to-year differences in the capture methodologies used can affect the year-specific probability of capture for an individual, further necessitating the need for sampling rates/capture probabilities to be estimated freely for each year.

Taken together, the data used in this analysis comes from a series of field studies not directly designed to assess population trends and it is therefore unclear whether repurposing this data for the current analysis impacted estimated population trends. From the global dataset a subset of data was used in the model which affected what can be estimated in the model (e.g., age/size selectivity was not estimated, shared mortality and sampling rates for both sexes). However, because similar methods were used in most years and only adult captures were included, we believe the restrictive use of the subset of data to be reasonable.



Table 1. Summary of trap effort and turtles catches in Revelstoke Reach, 2010 to 2016. Data for 2010 and 2011 are estimated from Basaraba (2014). Hand capture methods includes hand and hand held net. Basking traps were used in 2010 only. See Basaraba (2014) and Wood et al. (2016) for maps of trapping locations

		2010/ 2011	2012	2013	2014	2015	2016	2017	Totals ¹	Total Ind. ¹	
All Recorded Captures	Total Caps	Female	81	15	17	18	26	29	11	197	136
		Male	13	13	15	37	24	25	1	128	93
		Unclassified	93	0	9	0	20	31	0	153	178
	Total		187	28	41	55	70	85	12	478	407
	No. Marked	Female	45	17	23	26	22	45	0	178	178
		Male	28	13	22	40	18	25	0	146	146
Total		73	30	45	66	40	70	0	324	324	
Mark-Recapture Analysis	Total Caps	Female	47	14	14	15	24	28	10	152	110
		Male	12	12	14	31	23	24	2	118	91
		Total	59	26	28	46	47	52	12	270	201
	No. Marked	Female	41	5	12	8	23	20	1	110	110
		Male	12	6	13	23	18	19	0	91	91
		Total	53	11	25	31	41	39	1	201	201
Trap Effort Summary									Total Hours		
Capture	Cap. Method	Hand, Hoop, Basking	Hand, Hoop	Hand, Hoop	Hand, Hoop	Hand, Hoop	Hand, Hoop	Hoop, Basking			
	Trap Effort (hrs)	.	2446.7	3337.87	3230.52	1678.2	4936.55	NC ²	15629.84		
	Basking Traps	8	N/A	N/A	N/A	N/A	N/A	7			
	Hoop Trap Locations	34	17	57	36	11	38	10			

¹Totals refers to total captures; Total Ind. Indicates the number of individuals. ²NC = not calculated

Turtle Age Estimation

Assigning an age to a turtle can be difficult unless it is known from birth, which is not the case in the current study. To overcome this, we applied the methods of Armstrong and Brooks (2012) and Dolph (2017) to determine age of male and female turtles in our population. The Von Bertalanffy growth model was used to predict expected carapace length at age (L_a) and can be represented with following the form,

$$L_a = L_{\infty} \cdot (1 - e^{-ka})$$

where a is the age in years, k is the growth rate and L_{∞} is the asymptotic size. Sex-specific growth rates were used by employing sex-specific growth rates and asymptotic sizes. Initially, growth rates from Dolph (2017) were considered. However, revised growth rates and asymptotic lengths parameter values were determined to be needed due to the fact that the Western Painted Turtle population in Revelstoke Reach is both larger and longer lived than the population studied by Dolph (2017). Revised growth curves are presented below in the results.



Population Model

The population model assumes that all turtles in Revelstoke Reach comprise a single, geographically closed population (i.e., no immigration or emigration) and that all turtles captured in Revelstoke Reach, irrespective of capture location (i.e., in or out of the drawdown zone) were considered as a single population for the purposes of assessing trends. Turtles are long-lived species; therefore, distinct demographic segments of the population may be undergoing differing trajectories depending on the number of turtles born into the population and age-specific mortality rates. The current analyses consider these potential differences by reconstructing the population size across age and time independently for both sexes. Doing so allowed for the estimate of trends in the adult population as well as trends in the number of new individuals entering the population (recruitment). The future viability of the population was then assessed by projecting the estimated age structured population forward in time based on the continuation of estimated trends in recruitment. Additional future scenarios were also considered by making plausible alterations to the current recruitment trends.

The best-case outcome of the model would show a population that is viable and persists at or above current levels 40 years into the future (i.e., the current estimated life span of turtles in Revelstoke Reach, which is considered conservative [see COSEWIC 2006]). A worst-case outcome of the model would be that the population is declining, and more specifically, that the mature-aged females are declining. The viability of a turtle population is largely dependent on the number of mature females that can lay eggs, a decline in this demographic could have detrimental effects on the viability of the population in Revelstoke Reach.

Painted turtle population abundances at age and time were estimated using an integrated age-structured mark-recapture model (Coggins et al. 2006; Challenger et al. 2017). The method combines attributes of a traditional Jolly-Seber mark-recapture model (Jolly 1965; Seber 1965; Schwarz 2001; Williams et al. 2002) with virtual population analysis (VPA), a population reconstruction method widely used in fisheries stock assessments (Hilborn and Walters 1992). The model operates in discrete time, creating a virtual reconstruction of sex-specific abundances across age and time that best match the observed capture rates over sex, age, and time for the unmarked, and marked populations within the assessment period (i.e., 2010-2017). Unknown parameters for the model include the number of individuals entering the population, both historically and within the assessment period, age-specific mortality rates, recruitment into the first age class, and sampling rates (used to derive capture probabilities). Unknown parameters were estimated by minimizing the discrepancy between observed and predicted catches, which were predicted from the VPA portion of the model. The model is a direct application of the spatial age-structured mark-recapture described by Challenger et al. (2017), with the spatial component being used to model sexes with transitions between spatial components (i.e., sexes) removed. This model was developed through a collaboration between LGL and UBC on behalf of Habitat Conservation Trust Fund and the Fraser River Sturgeon Society.

Briefly, a VPA is a cohort modeling technique used to reconstruct numbers at age (both current and historical) based catch-at-age data and mortality rates (Hilborn and Walters 1992). It is virtual in the sense that age-specific abundances are not directly observed, but are inferred or back-calculated to have been a certain size in the past to best support the observed catches over sex, age and time, based on the estimated recruitment, sampling rates and mortality-at-age rates. As such, the VPA an age structured Leslie matrix and represents the demographic model used to make population projections. The integration with the mark-recapture statistical models is accomplished by including the VPA predicted catches in the model likelihood. This is accomplished by separately tracking unmark and marked populations with transitions between populations based on tagging records (Figure 1). The unmarked and marked predictions derived from the VPA component are then directly included in a composite likelihood, which separately considers



entrants into the unmarked population (log normal catch-at-age statistical model) from recaptures in the marked population (Cormack-Jolly-Seber type model) for a given set of parameter values, some of which are shared between likelihood components (the full likelihood specification is available in Challenger et al. 2017).

Integrating a VPA-type analyses into the statistical model confers advantages over more traditional Jolly-Seber type approaches for population assessments. The primary advantage is that the formulation allows for population abundance estimates to directly enter the likelihood. Doing so allows the analysis to directly consider the likelihood of different population sizes. In contrast, Jolly-Seber type approaches estimate population abundances as a derived variable (e.g., see Schwarz 2001; Link and Barker 2005). Jolly-Seber type of approaches depend on the accuracy of the capture probability estimated to infer population size. This can lead to large biases in estimated abundances if sampling assumptions are violated, especially if recapture rates are low. In contrast, integrated population models, such as the analysis model, considers information from multiple sources in addition to directly including population size estimates in the model likelihood. This allows for more robust and precise estimates of abundance and demographic processes relative to non-integrated models (Besbeas et al. 2002; Tavecchia et al. 2009; Abadi et al. 2010a; Schaub and Abadi 2011).

The inclusion of the VPA component in the statistical model also provides important constraints on the range of feasible population sizes, as well as year-to-year changes in population sizes by age, making estimates of population size less sensitive to sampling assumptions. For example, if 15 older individuals (e.g., Age 25+) were first tagged near the end of the experiment, these untagged individuals would have had to also been alive at the start of the experiment given their age. The age structuring provided by the VPA enforces this constraint by explicitly including these individuals in the model states (i.e., sex-specific abundances over age and time). By limiting when new individuals could have entered the population, the possible population state-space is constrained thereby limiting the range of likely population size estimates.

Conversely, Jolly-Seber type abundance models cannot make direct use of age-at-capture information to constrain estimates. New marks are interpreted simply as recent births or immigration without any direct restrictions on when those births would have had to occur (i.e., “recent” could be between the last recent and current time or occurring at an earlier point in the experiment missed during sampling). For example, in Jolly-Seber type models, the probability a newly tagged individual “entered” the population between the previous and current sampling periods will be the same regardless of whether the captured individual is 5 or 25. This is not the case in age structured model. Jolly-Seber type based abundance models are also highly sensitive to sampling assumption violations, especially ones that that affects the accuracy of capture probability estimates. In Jolly-Seber type abundance models the accuracy of capture probability estimates not only affect estimates of the overall population size, but the estimated timing of entry of new individuals into the population, therefore any estimated population trends.

The VPA portion of the model operates in discrete time and is a state-space implementation using separate age-structured population matrices to keep track of the unmarked and marked populations for both males and females (Figure 1). These matrices are populated starting with the first age class (i.e., Age 1) then tracking the cohort to the final age class (i.e., Age 40). Recruitment into the first age class represents the number of turtles that hatch and survive through to the start of the first year of life and is treated as an unknown parameter. Recruitment only occurs into the unmarked population (Figure 1). Recruitment is also estimated separately for females and males and assumed to arising from a log normal distribution (Figure 2). The use of log normal for the prior distribution accommodates the possibility of extreme recruitment



events that may occur in the wild. The variability of the recruitment prior was fixed ($\sigma = 0.75$), but a hyperprior was placed on the mean allowing a large range of possible recruitment values to be covered (Figure 2). For example, under a hyper prior value of $\mu = 5$ a recruitment value of 200-500 per sex is still quite probable, which would translate to a total recruitment event of 400-1000 Age 1 turtles within a given year, which is highly unlikely scenario given the size of the population. As such, higher values of μ were not considered.

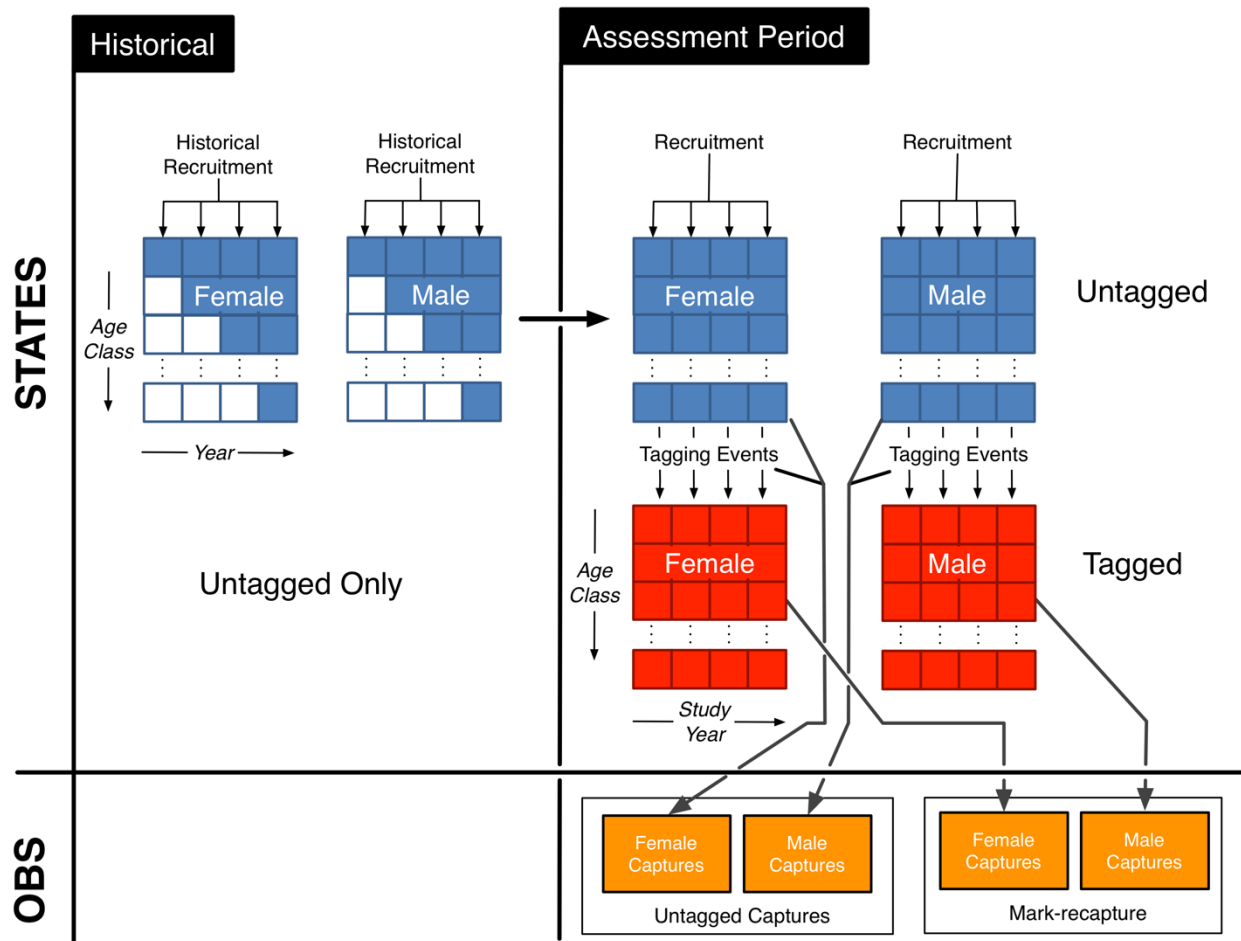


Figure 1. Illustrative schematic indicating underlying model states, transitions between states, and functional relationships. Note that illustration does not show time steps, see Challenger et al. 2017 for more detailed schematics of model functioning.

After recruiting into the first age class, each sex-specific cohort is then taken through yearly time steps where further demographic processes (i.e., mortality, aging and transitions from unmarked to marked populations) are applied. Recruitment always occurs at the start of each time step, followed by transitions from the unmarked to marked populations with aging and mortality occurring at the end of each time step. Instantaneous mortality rates represent the sum of all hazards faced individual turtles throughout their life (e.g., natural as well as anthropogenic) as they age from the first to terminal age class. Age specific mortality rates (M_a) were used based on a Gompertz mortality curve:

$$M_a = \lambda e^{\gamma a}.$$



Gompertz mortality curve predicts the mortality rate for age a , based on λ , the mortality rate at Age 1, and γ , the rate of exponential increase in mortality with age (see Pletcher 1999). This formulation was chosen as it was found to be a good predictor of mortality in other Painted Turtle populations (Warner et al. 2016). Temporal effects on mortality were not considered in the current study and the same age-specific mortality curve was used for both sexes due to limitations in the available data. For consistency with other published results (e.g., Warner et al. 2016) we present log mortality at age values, which can be determined as

$$\log(M_a) = \log(\lambda) + \gamma a.$$

Age-specific survival probabilities (which are also presented) can be approximated from the mortality rate estimates as

$$\phi_a = \log(-M_a)$$

where ϕ_a is the probability of an individual alive at age a survives to age $a + 1$ (Carey, 1993).

Abundance estimates are determined from the VPA component of the model. Estimates that included all modelled age classes are only available within the study period (i.e., 2010 to 2017), with a subset of age classes available for years before the assessment period (Figure 1). One historical age class is lost for each additional year “back calculated” due to the fact that partial historical reconstruction was used. VPA abundances can be seeded by treating recruitment as an unknown and forward projecting to determine numbers at age and time, known as “forward projection” or “backwards projection” can be used where terminal abundance at age and time are treated as an unknown and projected backwards (Coggins et al. 2006). A “forward propagation” technique was chosen as it allowed for single recruitment model to be used to generate all unknown abundances resulting in a simpler model with fewer assumptions (Challenger et al. 2017). This resulted in an upper triangle sex-specific population matrix prior to the start of the assessment period (Figure 1), which limits historical abundance estimates to a subset of age classes available for a given historical year.



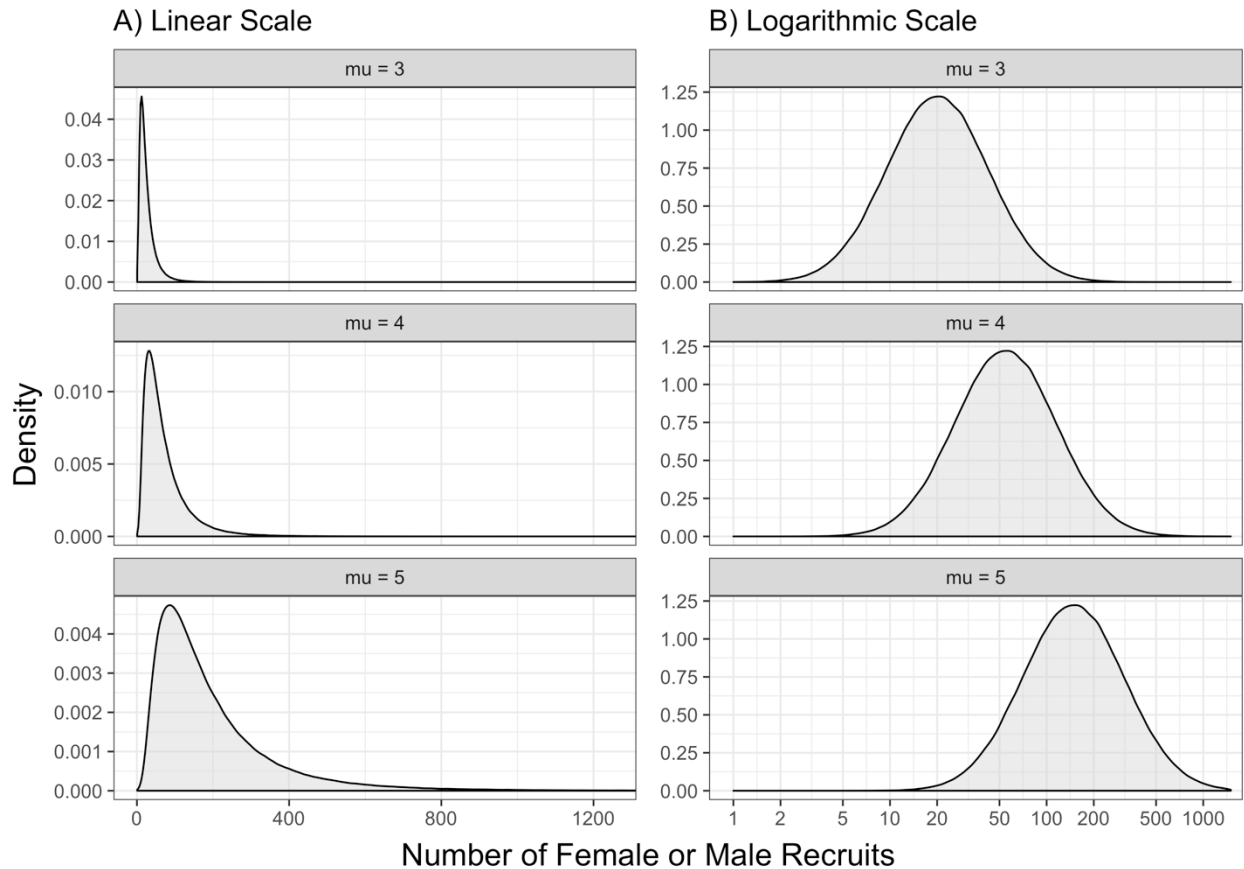


Figure 2. Log-normal prior distribution for sex-specific recruitment for the range of possible values of μ and $\sigma = 0.75$ (mean and variance, respectively). A uniform hyper-prior was placed on μ allowing it to take any value between 2.5 and 5 with equal probability providing a large range of possible recruitment values.

The high granularity of the VPA component allows for a large array of demographic breakdowns to be generated. Examples of demographic breakdowns include total population (i.e., both sexes and all age classes), sex-specific abundances, any combination of age classes, as well as combinations of sex and age class. Furthermore, by estimating male and female recruitment separately, estimates of yearly sex ratio may also be generated as a derived parameter. Population projections (e.g., 5, 10, 20, and 40 years) into the future were based on current age-structure results along with mortality rates and hypotheses about recruitment (e.g., a continuation of the currently recruitment trend rates, increases, and decreases in recruitment).

All unknown parameters were estimated using a Bayesian estimation technique with the statistical model implemented in Automatic Differentiation Model Builder (ADMB), which is a “programming framework based on automatic differentiation, aimed at highly nonlinear models with a large number of parameters” (Fournier et al. 2012). Data preparation and results processing were conducted in the R computing environment (R Core Team 2017). ADMB is an efficient and stable parameter estimation framework well suited to high dimension ecology problems such as estimating age-structured matrices (Maunder et al. 2009; Bolker et al. 2013). The full model specification can be viewed in Challenger et al. (2017). The only changes made in this study from Challenger et al. (2017) study were: the use of spatial components to model sexes (without transitions between components); the Gompertz mortality at age curve; freely estimated yearly sampling rates, as opposed to a function of effort, due to the lack of consistent records



on sampling effort; constant age-specific capture selectivity due to lack of sample size and data restriction that only included only adult turtles; and a hyperprior added to the log-normal recruitment (see Figure 2). Because age-specific capture selectivity was not included, the accuracy of the model results depends on the age structure of sampled adults accurately reflecting the age structure of adults in the population. Metropolis-Hastings Markov Chain Monte Carlo functionality of ADMB was used to generate a posterior sample. A burn-in of 50,000 samples and a thinning rate of one in every 900th sample was used to remove any signatures of auto-correlations between population estimates. After burn-in and thinning, a total of 10,000 posterior samples were retained, with each posterior sample representing a unique VPA realization associated recruitment, age-specific mortality and sampling rates. Each posterior VPA sample was processed to determine abundances estimates, trends in the adult population (e.g., average change per year), and linear trends in recruitment in order to produce the posterior distribution of each derived variable.

Results

Revised Growth Curve and Aging

Growth curves from Dolph (2017) were updated to better match the study population (Figure 3a). Asymptotic female carapace length (L_{∞}^F) was set to 220 mm to match observed maximum size (see IDs F201; Appendix A: Capture Data). Female growth rate was then estimated to be $k^F = 0.148$ based on the observation that the smallest gravid female observed in the population had a carapace length of 177 mm, and the youngest gravid females are about age 11. This revised growth curve was then used to convert female lengths at first capture (Figure 3b) to the ages at first capture used in the analysis (Figure 3c). Less information was available for males so the $L_{\infty}^F:L_{\infty}^M$ and $k^F:k^M$ ratios observed in Dolph (2017) combined with the estimated female values were used to set asymptotic male carapace length (L_{∞}^M) to 205 mm and male growth rate (k^M) to 0.073. These parameter values were then used to convert male lengths at first capture (Figure 3b) to the ages at first capture (Figure 3c). Ages at first capture are provided in Appendix A.



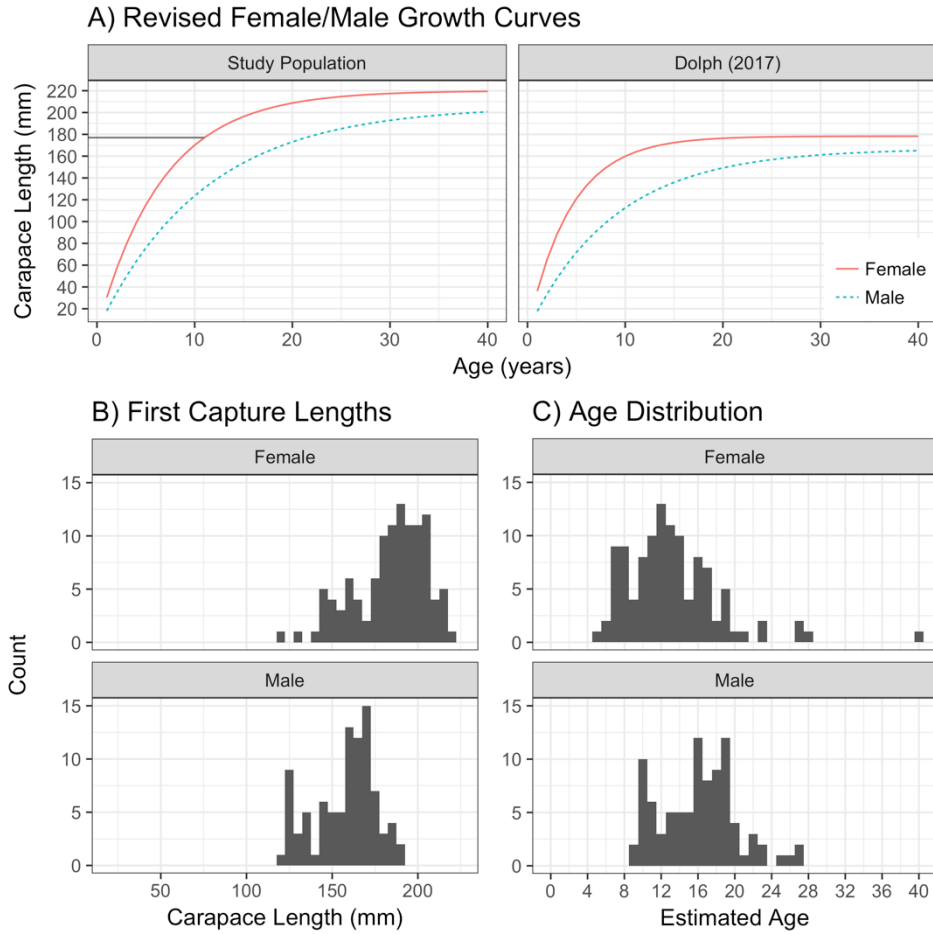


Figure 3. Study population growth curves and estimated age at first capture. (A) Revised Western Painted Turtle population growth curve used to convert lengths at first capture (B) into estimated age at first capture (C). A total of n=91 males and n=111 females were used.



Sampling Rates, Mortality and Recruitment

The instantaneous sampling rates were estimated for each year (Figure 4a), higher rates indicate years that may have had higher effective sampling effort which could mean more efficient sampling practices, or a combination of the two. Age-specific mortality estimates showed the lowest uncertainty within the age range that had the highest proportion of sampling (green shading; Figure 4b), with larger uncertainty for the youngest and oldest age classes. The mortality curve was based on fitting a polynomial to log mortality rates and can also be presented as the probability of surviving from one year to the next for any given age class (Figure 4c). The highest uncertainty related to mortality in the oldest age classes, of which there were few observations (see Figure 3c). Uncertainty in the youngest age classes (i.e., < 5) may not indicate true uncertainty as this part of the curve was based on older individuals.

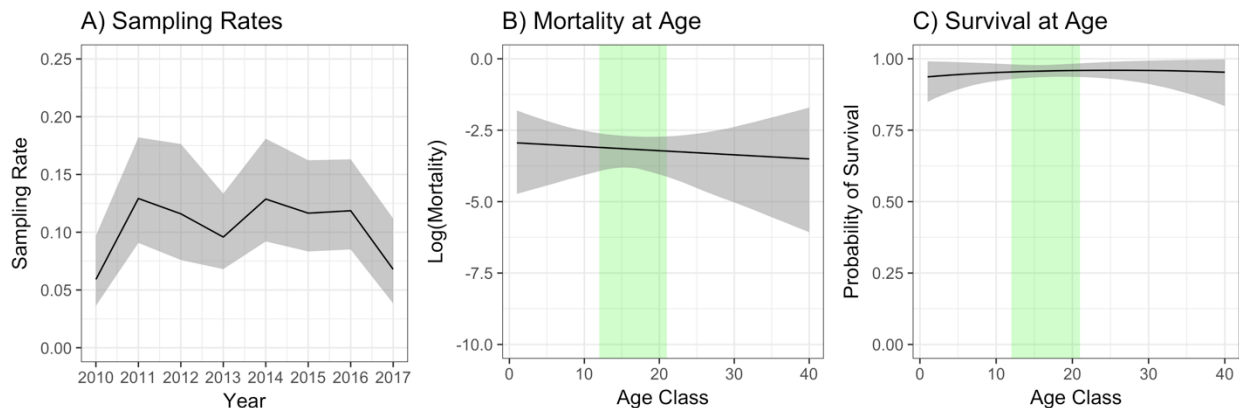


Figure 4. Estimates of study sampling rates and yearly mortality rates. (A) instantaneous yearly sampling rates used to predict the probability of capturing an individual turtle in a given study year; (B) estimated mortality at age; and (C) survival at age curves. Shading indicates 95% credible intervals. Green shading in panels (B) and (C) indicates the age range that comprised 50% of the observations.

Estimates of historical and study period recruitment were largely informed by the number of age specific untagged captures, sampling rates and mortality at age rates (Figure 5). Prior to ~ 1985 for females and ~1981 in males, the estimates have much higher variability with variance and mean values similar to the prior distribution for recruitment. A similar trend occurs after 2011 for females and 2005 for males. Recruitment estimates in these periods are largely uninformative covering the range of values specified by the prior distribution on recruitment. This indicates that there is likely little information in the observed captures about these recruitment years. The oldest uninformative years are likely the result of few observations in the older age classes (Figure 3), while the more recent uninformative years result in the lag in time for age 1 recruits to grow large enough to enter the sampling program. It was possible to generate informative estimates farther back for males due to the older age distribution of captures (Figure 3c). Furthermore, informative estimates of female recruitment could be generated for more recent years than males due to the faster growth rates of females (Figure 3a), which will result in females becoming exposed to sampling at earlier ages. Finally, informative recruitment years showed year-to-year variability with a possibility of a decrease over time. This possibility of a trajectory in male and female recruitment was further investigated in the next section.



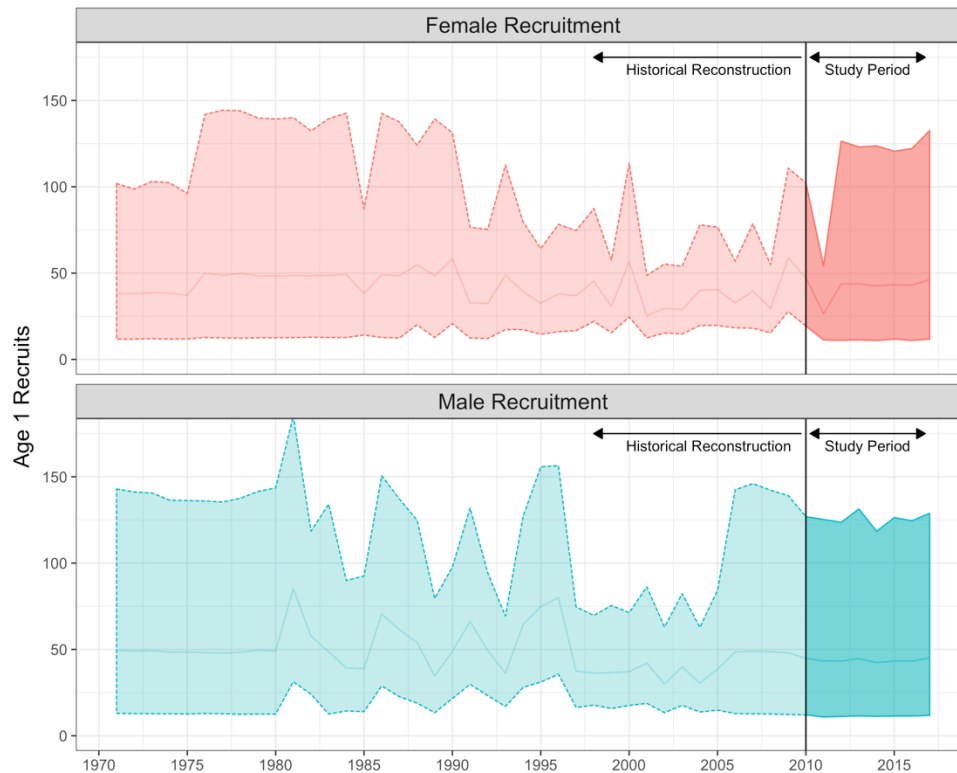


Figure 5. Estimated female and male age 1 recruitment. Historical recruitment was reconstructed based on estimated abundances within each age class and the estimated mortality rates. Shading indicates 95% credible intervals.

Population Size, Demographics and Trends

The estimates of the adult population size (age 10 and older turtles) were generated for each study year (Figure 6). Overall, the total and sex-specific abundances showed a similar steady decline through the study period (Figure 6a). Total abundance is estimated at approximately 890 adult turtles in 2010, declining to roughly 630 adults by 2017. The average yearly change in the number of adults (i.e., change in the number of turtles per year) was used to quantify the population trend and was estimated for each posterior sample of age 10+ abundances resulting in the posterior distribution for linear trends (Figure 6b). The total population was estimated to decline by a total of 36 turtles per year (95% CI: -49.7, -24.9 turtles per year), with sex-specific declines showing similar levels of yearly decline in turtles (95% CI – females: -24.3, -8.6 turtles per year; males: -28.9, -13.5 turtles per year). Comparing the population size at the start and end of the study period, indicated an estimated 29.3% decline in the total population (95% CI: -39%, -19%) with similar levels of decline exhibited by both sexes (95% CI – females: -38.0%, -15.3%; males: -41.6%, -19.6%).



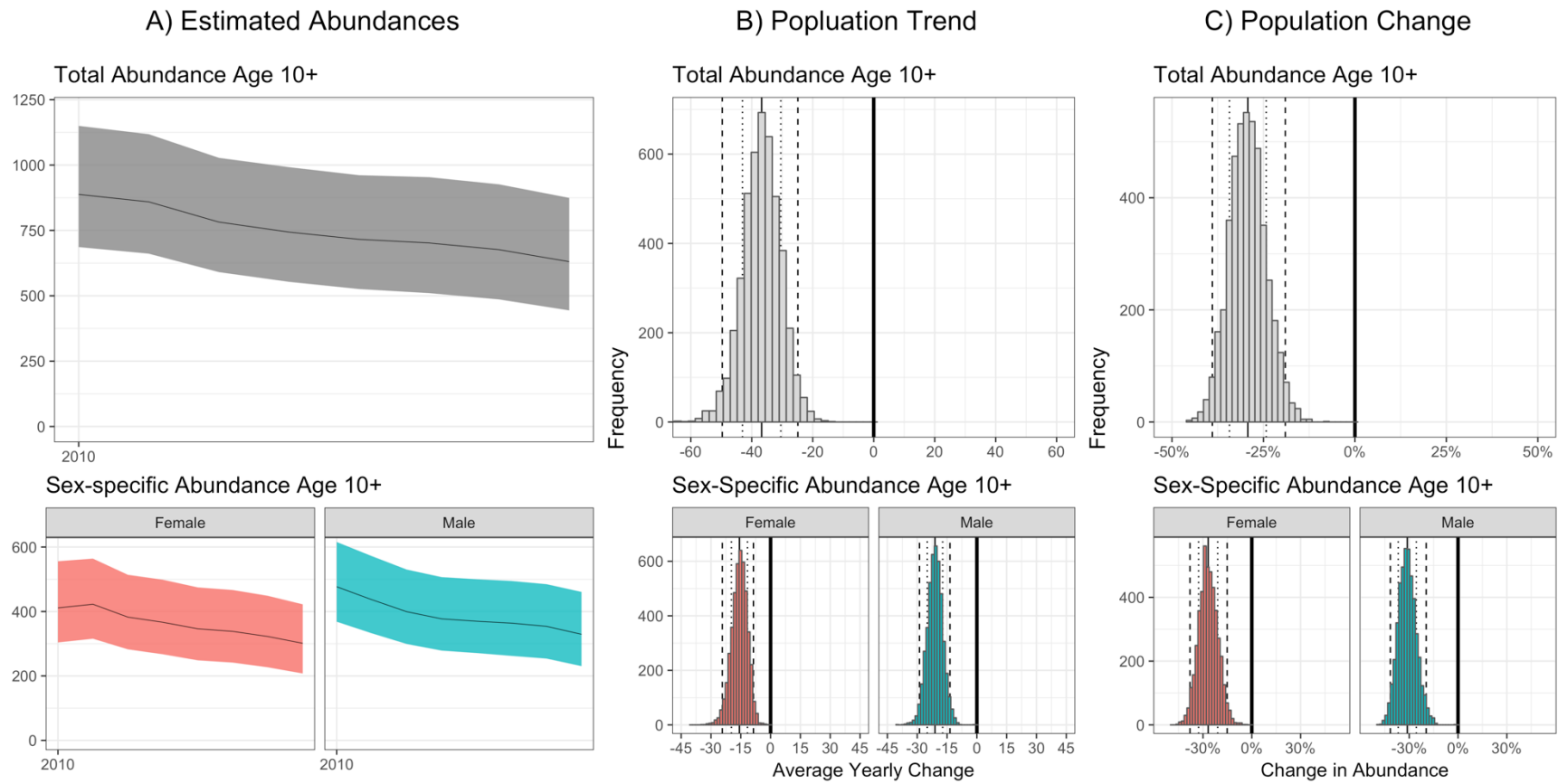


Figure 6. Estimated total and sex-specific adult abundances within the study period. (A) age 10 and older turtles within the study period (2010 to 2017), (B) the posterior distribution of estimated linear yearly trends in abundances and (C) per cent change in population size over the study period. Shading in panel (A) indicates the 95% credible intervals for yearly abundances. Dotted lines in panel (B) and (C) indicate one standard deviation from the distribution mean, dashed lines indicate the 95% credible intervals, and thin vertical line indicates distribution mean. Thick vertical line in panels (B) and (C) indicates the null hypothesis of no trend.



A mix of methodologies was used during the study period, therefore sensitivity of trend estimates to methodology changes was assessed by repeating the analyses under different data subsets (Figure 7). Data subsets include turtles that were only notched, turtles that were notched with a telemetry transmitter, and survey years when only LGL/ONA conducted the field research. For all data subsets, the population trend estimated was negative, with the mean of the posterior at least one standard deviation away from zero (i.e., no trend), indicating potential evidence of a decline. For three of the four data subsets (i.e., Figure 7a-c) the mean of the posterior was > 2 SD from zero, indicating stronger evidence for a decline. Finally, for two of the four data subsets (i.e., Figure 7a,c) the mean of the posterior was > 5 SD from zero indicating an exceedingly small probability that population was stable during the assessment period.

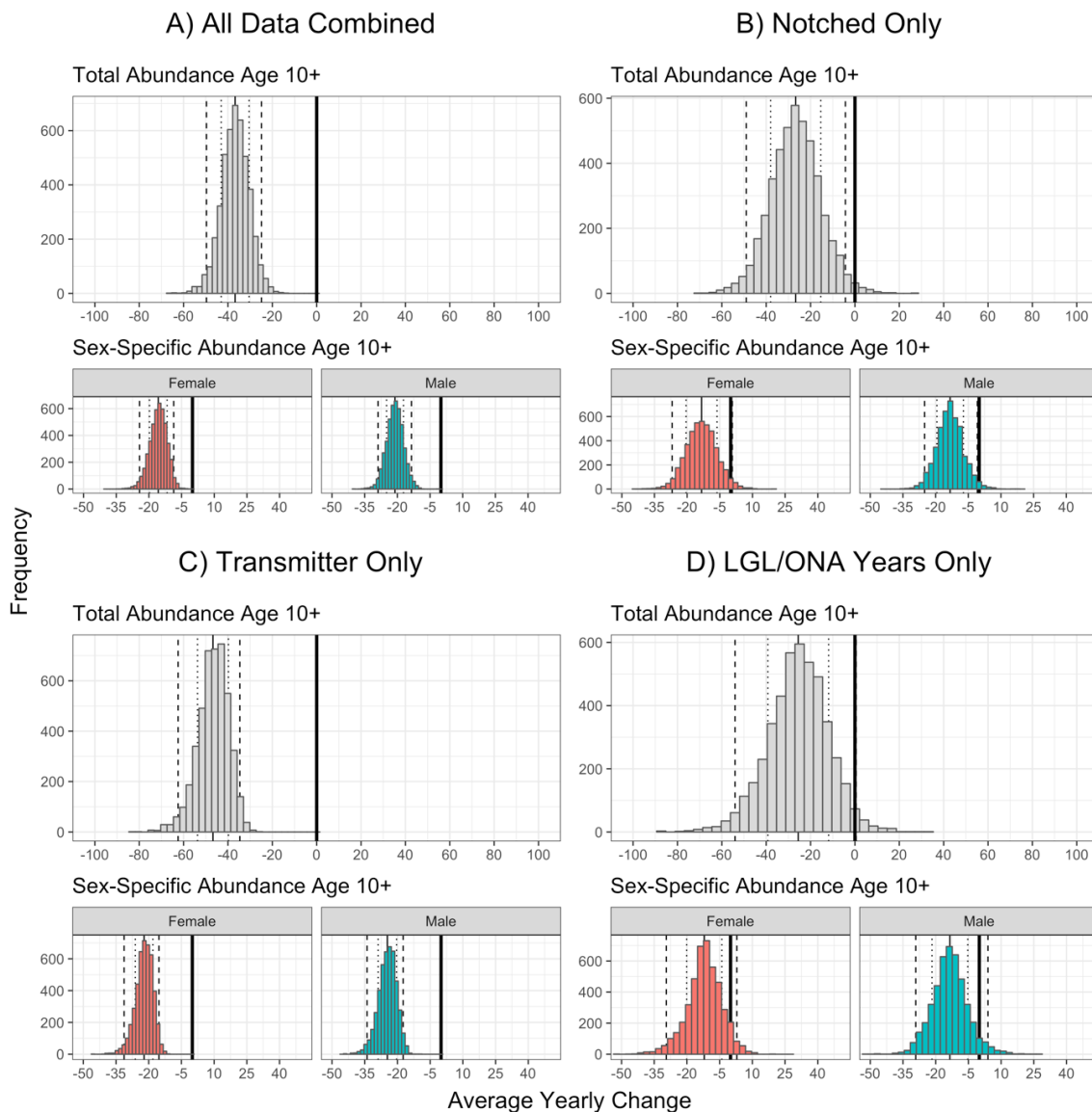


Figure 7. Estimated average yearly change in the population size under different data subsets. A) all available data, B) turtles marked only with notches, C) turtles marked with a notch and a transmitter, and D) study years were only LGL/ONA conducted the sampling (2014-2017).



It should be noted that the yearly population estimates in Figure 6a were generated from the posterior sample of VPA abundances. While the estimates clearly show a trend, the credible interval does not indicate uncertainty in the trend itself, but rather the uncertainty in the total number of adults at each study year. Inspecting a random selection of posterior samples reveals that most posterior population projections featured a similar trend, but that there was uncertainty over the true number of adults (Figure 8). As such the results indicate a higher confidence in the estimated trend rather than the estimate of the absolute number of turtles.

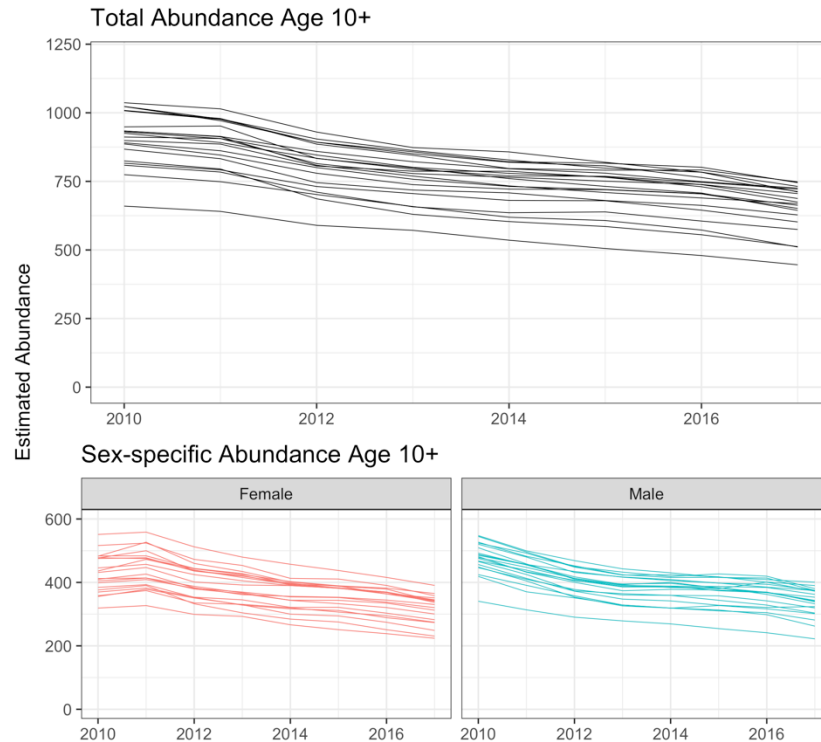


Figure 8. Population trajectories from a random selection of posterior samples.

To provide more context for this estimated decline, historical and study period abundances by demographic category and sex are also provided (Figure 9). The historical reconstruction assumes mortality rates by age in the historical period were the same as the study period. The reconstruction is also a partial reconstruction were estimates for the oldest age class (i.e., age 40) only start in the study period. As such, younger demographic categories can be reconstructed farther back than older categories. Overall, the category containing the majority of mature reproductive individuals (i.e., ages 16–32) showed some of the strongest declines in the study period, while the juvenile age class (i.e., ages 6–11) showed earlier signs of a decline, especially for males. The youngest (i.e., ages 1–4) and oldest (i.e., ages 33–40) age classes were relatively stable. Reproductive female abundances are often considered critical to population viability, therefore estimates were further broken down for the female age ranges considered to be reproductive (Figure 10). While the younger age classes of reproductive females showed evidence of declines and increases within the study period, the ages that can be expected to be the most fecund (i.e., ages 21–26) showed a prominent and consistent decline within the study period. The oldest reproductive age class (i.e., ages 27–32) also showed a similar prominent decline.



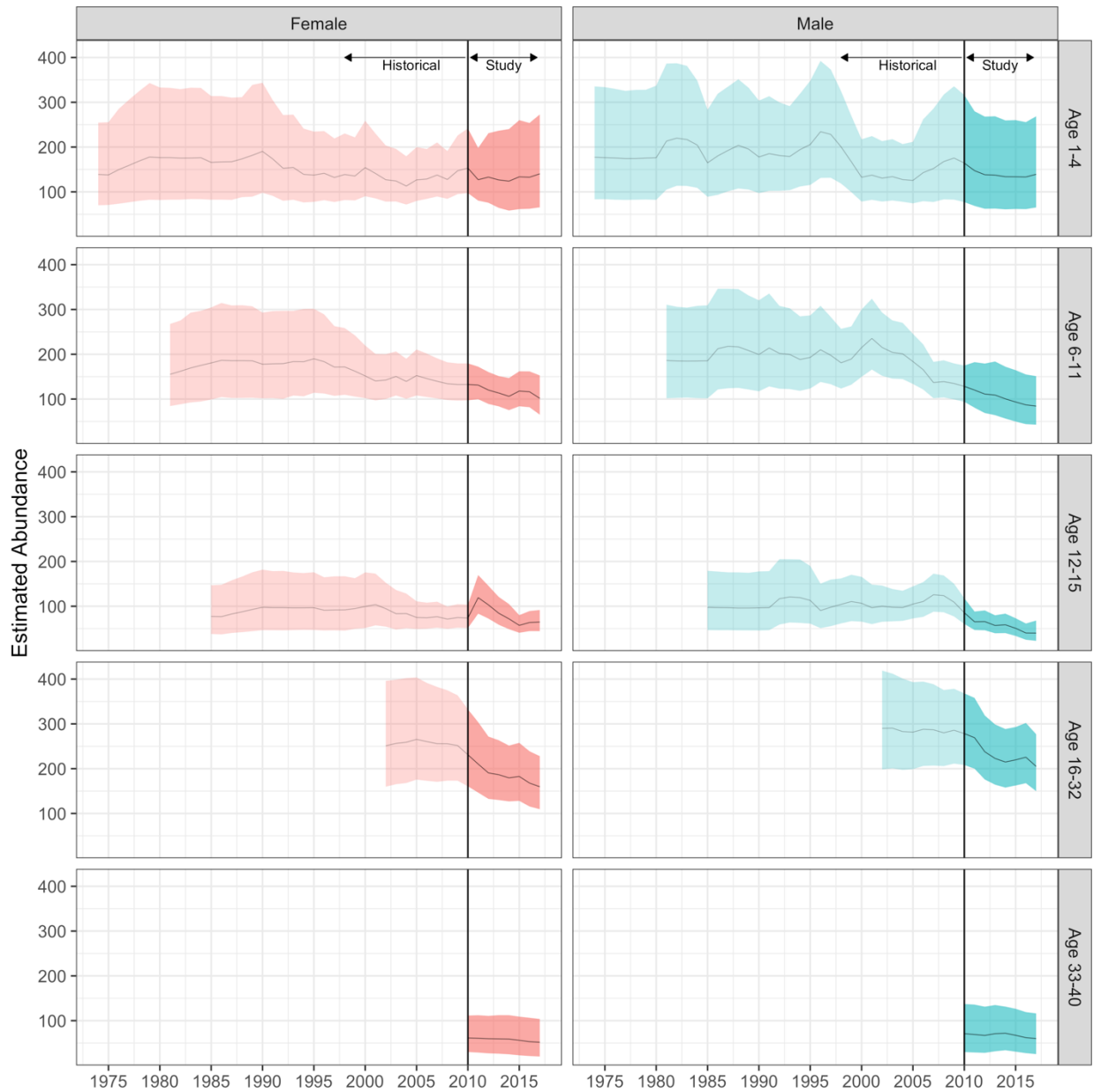


Figure 9. Estimated historical and study period abundances of Western Painted Turtles for different demographic breakdowns of female and male abundances. A partial historical reconstruction was used to generate estimates prior to the start of the study period in 2010. Shading indicates 95% credible intervals. Darker shading indicates study period where lighter shading represents the historical reconstruction.



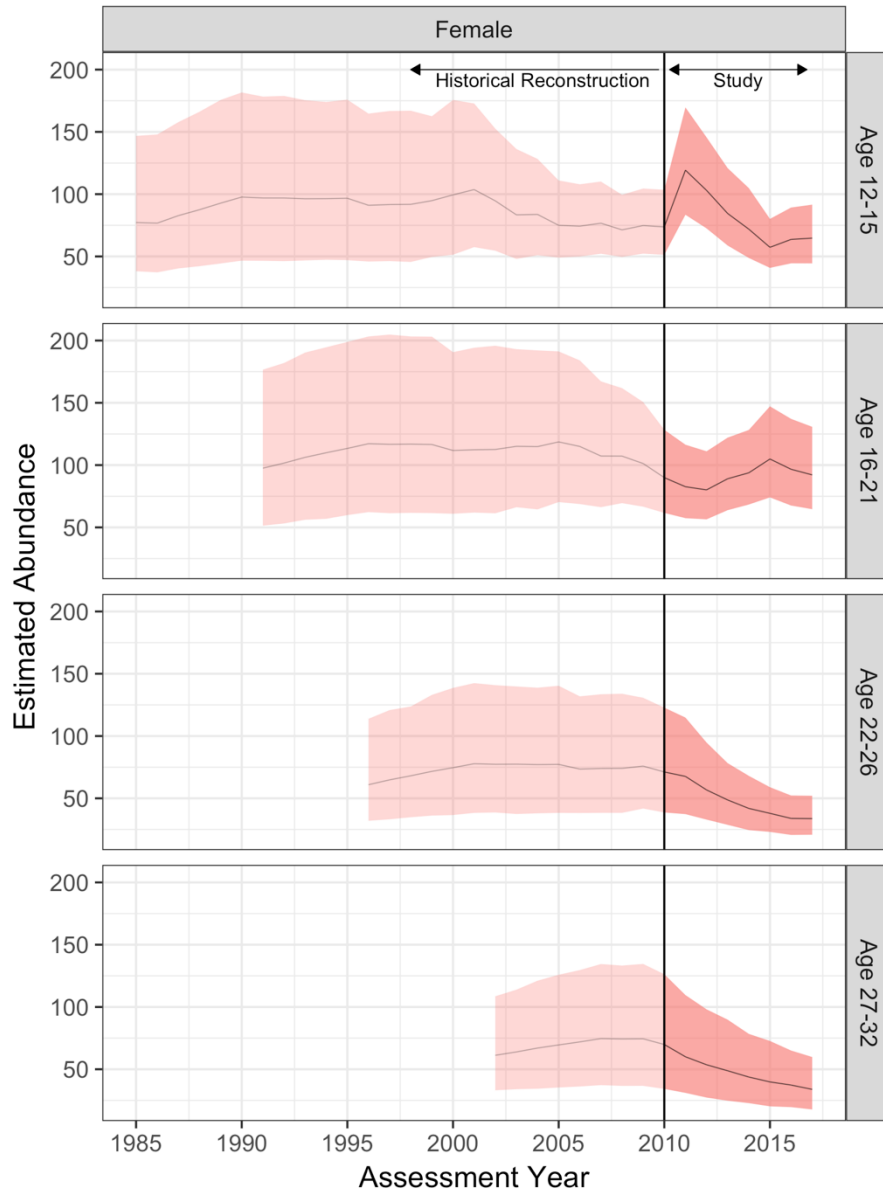


Figure 10. Estimated historical and study period abundances of Western Painted Turtles for different demographic breakdowns of reproductive females. A partial historical reconstruction was used to generate estimates prior to the start of the study period in 2010. Shading indicates 95% credible intervals. Darker shading indicates study period where lighter shading represents the historical reconstruction.



Projected Population Trends

Forty-year population projections were generated by first projecting recruitment into the future followed by projecting the sex- and age-specific abundances forward using projected recruitment and the estimated mortality-at-age curve (Figure 4b). Recruitment projections were created by first estimating the log-linear trend in the posterior recruitment sample (Figure 11a) and then projecting the trend forward based on the estimated trend within each posterior sample (see Figure 11b for the posterior distribution of recruitment trends). Only a subset of estimated recruitment years were believed to be informative, as such, the recruitment trend was only estimated within these years (see green shading; Figure 11a). Some of the uninformative years were also within the study period, or just before (see grey shading; Figure 11), the recruitment trend was projected from the end of the informative through the uninformative recruitment years within the study period and through the projection period. Estimated recruitment trends also indicated the potential for sex-specific trends, where male recruitment may be undergoing a larger decline (bottom panel, Figure 11b). As such, we considered projecting recruitment as following the average recruitment trend (top panel, Figure 11b), or the sex-specific trend (bottom panel, Figure 11b).

Within either approach (i.e., sex-specific recruitment trends or average recruitment trends) a total of three further recruitment scenarios were considered (average trend: Figure 12; sex-specific trends Figure 13):

1. Recruitment Scenario (1) continues the estimated log-linear recruitment trend (~ 1 per cent decline per year), this trend was continued from the informative years through the uninformative years and then through the 40-year projection period (herein referred to as Scenario 1).
2. Recruitment Scenario (2) considers an accelerated decline in recruitment of approximately two per cent per year (i.e., a doubling of Scenario 1) and is intended to represent a possible side-effect of the estimated decline in the reproductive females and is considered to be the most plausible scenario (herein referred to as Scenario 2).
3. Recruitment Scenario (3) considers the impact of stabilizing recruitment (herein referred to as Scenario 3).

Scenarios 2 and 3 were implemented by adding a constant offset to the estimated posterior log-linear slopes thereby shifting the posterior distributions (Figure 11b) to be either twice the current trend (Scenario 2) or to be centered on zero (Scenario 3).

Under these possible recruitment scenarios future adult population sizes were projected over the next 40 years (average recruitment trend: Figure 14; sex-specific recruitment trend: Figure 15). All three projection scenarios featured large uncertainty with a population increase or a population decreases over the next 40 years being plausible outcomes. While the total population projections were the same for either the average or sex specific recruitment trend, the sex-specific population projections did however differ, with males undergoing notable declines in some scenarios (i.e., bottom panel, Figure 15b). Scenarios with higher recruitment uncertainty also produced more uncertainty in projections of adult population sizes, due to the impact of a higher frequency of larger reproductive events (i.e., the variance of a log normal distribution is affected by the mean value). Scenarios that featured a decline in recruitment (i.e., scenarios 1 and 2) also showed lower recruitment variability due to recruitment being log-normally distributed. Under recruitment Scenario 1 the average posterior predictive projection indicated a population that has stabilized at a size similar to the size estimated at the end of the study period. Under recruitment Scenario 2, the average posterior predictive projection indicated a continuation of the population decline estimated in the study period, although at a reduced rate. Under Scenario 3, which features stable recruitment, the average posterior predictive projection indicated a potential population recovery to a level virtually identical to the population size at the start of the study period.



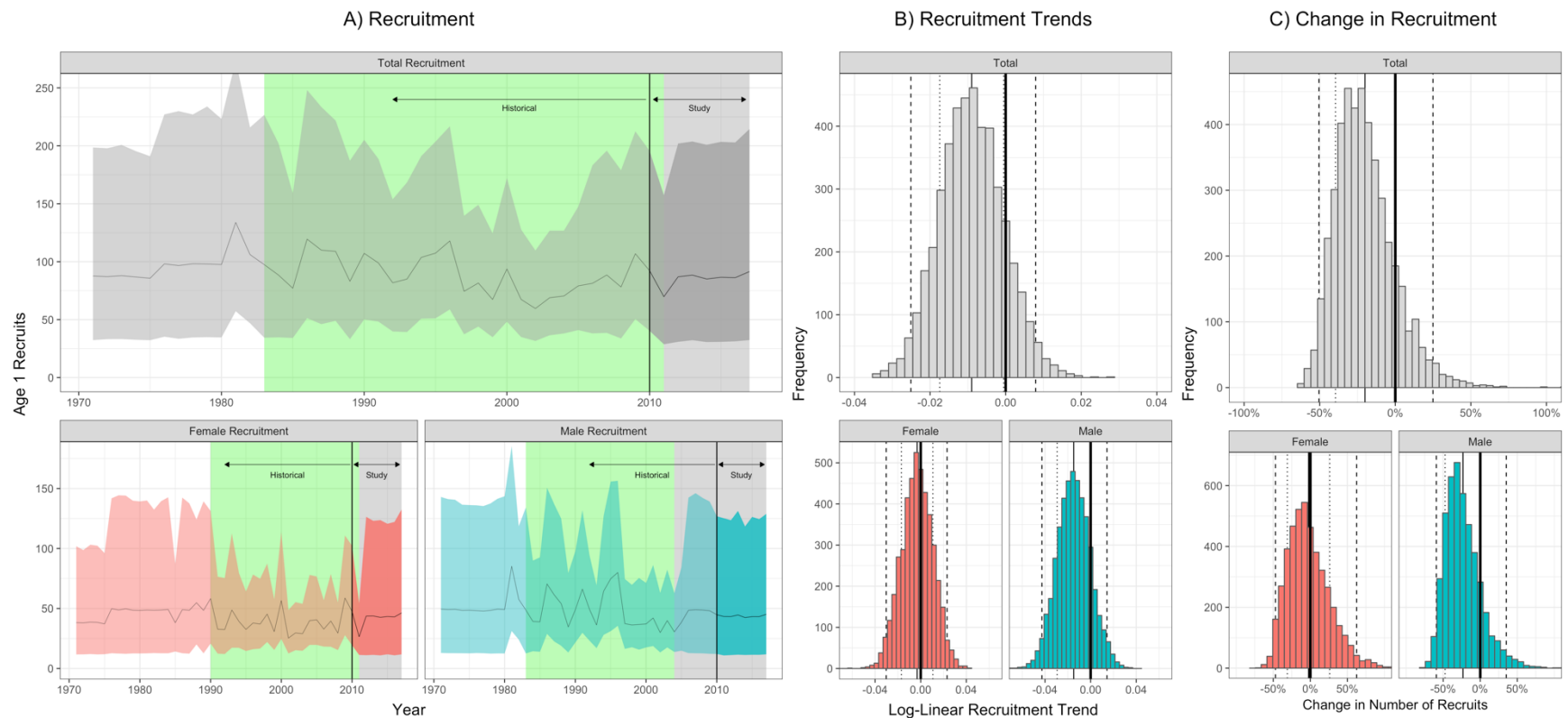


Figure 11. Estimated historical and study period recruitment (A) and trends in recruitment (B) and per cent change in recruitment (C) during the years deemed to provide informative estimates of which Western Painted Turtle recruitment (green shading). Dotted lines in panels (B) and (C) indicate one standard deviation from the distribution mean, dashed lines indicate the 95% credible intervals, and thin vertical line indicates distribution mean. Thick vertical line in panel (B) and (C) indicates the null hypothesis of no trend. Darker shading in panel A indicates study period where lighter shading represents the historical reconstruction.



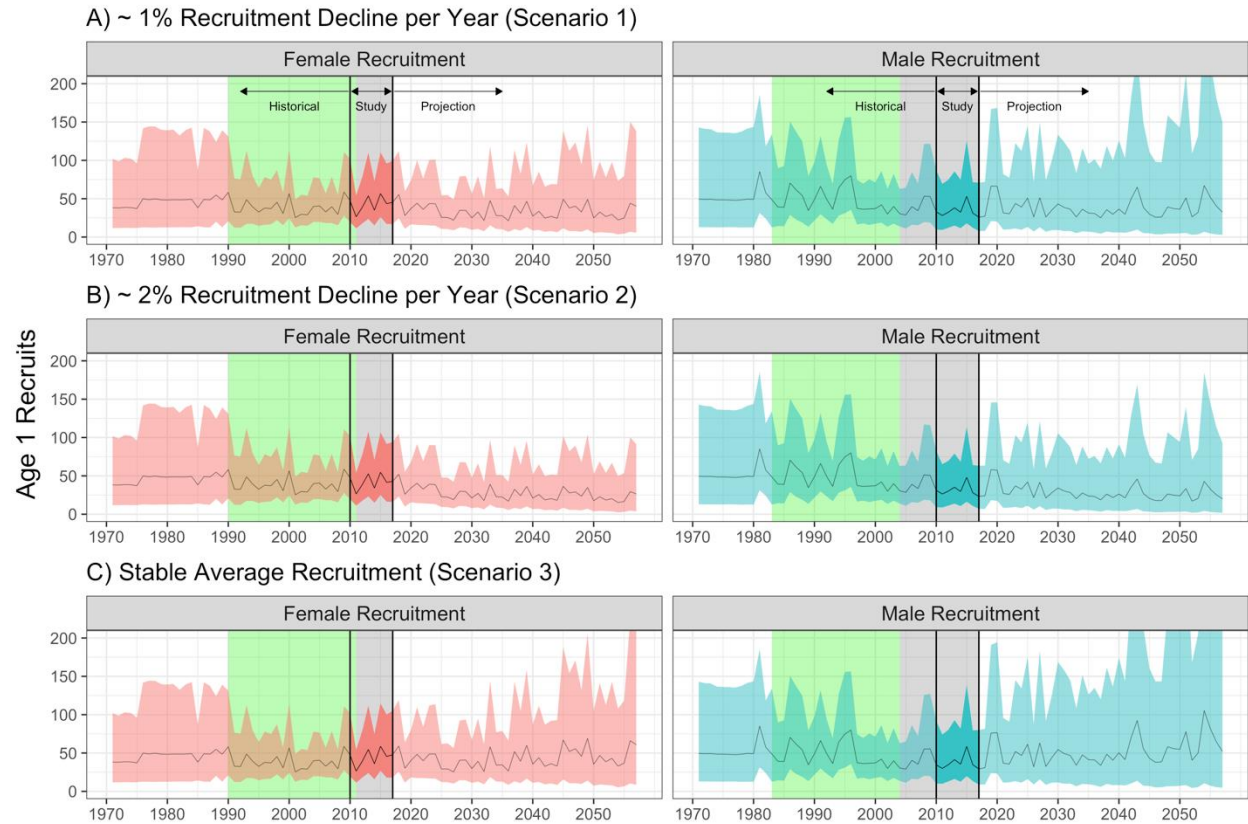


Figure 12. Projected male and female recruitment when sex-specific recruitment follows the same temporal trend. Three recruitment scenarios were considered. (A) Scenario 1: continuation of the current recruitment trend within the informative years (green shading), (B) Scenario 2: a doubling of the current trend, and (C) Scenario 3: stable recruitment. Green shading indicates recruitment years used to base the forward recruitment projections (all years after the green shading). Log-linear trends within the informative (green shading) period were projected into the uninformative years (grey shading) and onwards for the full projection period.



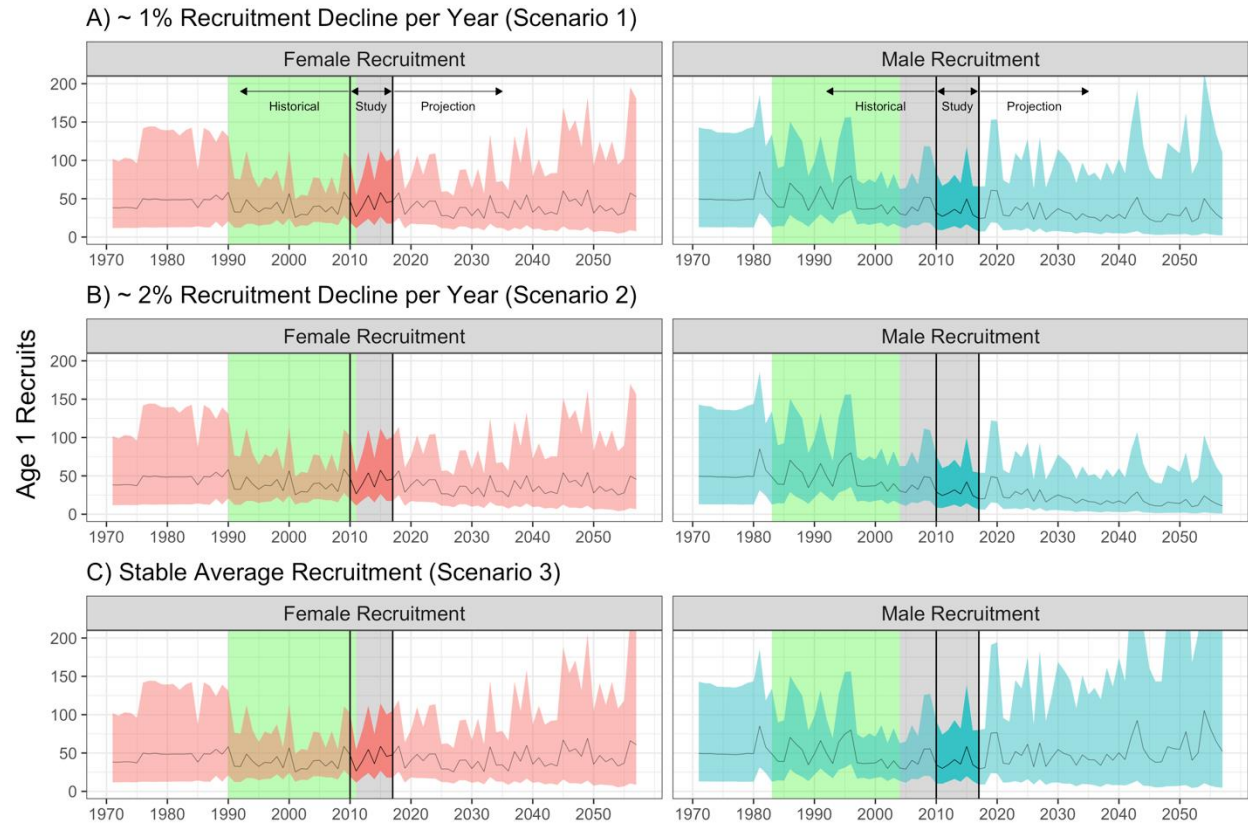


Figure 13. Projected male and female recruitment when sex-specific recruitment follows sex-specific temporal trends. Three recruitment scenarios were considered. (A) Scenario 1: continuation of the current sex-specific recruitment trends within the informative years (green shading), (B) Scenario 2: a doubling of the current sex-specific trends, and (C) Scenario 3: stable recruitment. Green shading indicates recruitment years used to base the forward recruitment projections (all years after the green shading). Log-linear trends within the informative (green shading) period were projected into the uninformative years (grey shading) and onwards for the full projection period.





Figure 14. Estimated (2010–2017) and projected (>2017) Western Painted Turtle population assuming sex-specific recruitment follows the same temporal trend. Three recruitment scenarios were considered. (A) Scenario 1: continuation of the current trend, B) Scenario 2: a doubling of the current trend and C) Scenario 3: stable recruitment. Grey shading in top panels indicates 95% credible intervals. Lighter shading in each panel indicates projected (modelled) abundance. Top panels: total population abundance; bottom panels: female and male abundances.





Figure 15. Estimated (2010–2017) and projected (>2017) Western Painted Turtle population assuming sex-specific recruitment follows sex-specific temporal trends. Three recruitment scenarios were considered. (A) Scenario 1: continuation of the current trend, B) Scenario 2: a doubling of the current trend and C) Scenario 3: stable recruitment. Grey shading in top panels indicates 95% credible intervals. Lighter shading in each panel indicates projected (modelled) abundance. Top panels: total population abundance; bottom panels: female and male abundances.



Discussion

An integrated population model was used to model Western Painted Turtle population dynamics, which provided a formal way to link changes in population size with demographic rates into a single analysis framework (Schaub and Abadi 2011). Typically, these types of analysis components are carried out separately, and then combined into a population matrix so that population may be projected forward in time (e.g., Jenouvrier et al. 2003). Conducting separate analyses does not make efficient use of the data, nor provide a formal way to account for uncertainty in the population projections. By combining both steps into a single framework, integrated population models, such as the one used in the present study, simultaneously make use of all available information resulting in more precise and robust estimates than would be obtained otherwise (Besbeas et al. 2002; Tavecchia et al. 2009; Abadi et al. 2010a; Schaub and Abadi 2011). Furthermore, the integration also provides a formal framework for providing estimates of uncertainty for the population projections.

An added benefit of the age structuring used in the VPA component of the analysis model (i.e., the demographic model) was that it also provided limits on the range of plausible population estimates by considering the age structure and age specific abundances as part of the model likelihood (Challenger et al. 2017). Classical approaches such as Jolly-Seber type models do not include either population estimates or age structuring in the modelled likelihood and are therefore much more sensitive to sampling assumptions (Schwarz 2001; Link and Barker 2005). As such, integrated models, such as the analysis model, can be expected to provide more robust and precise estimates assuming accurate aging and accurate sampling age structure information.

The results as presented are therefore reliant upon accurate aging of individuals at first capture and that the age structure of sampled adults accurately reflects the true age structure in the adult population. Restricting the main inference to adults minimized the potential impact related to aging uncertainty and size/age related catchability is likely to be much more consistent within this demographic grouping (Pike et al. 2008). That said, common trapping methods can produce different capture rates among size classes and between sexes, with juveniles being generally less catchable (Pike et al. 2008; Tesche and Hodges 2015; Gulette et al. 2019). Ideally, all captures, regardless of age could be included if size related differences in catchability could be accommodated using a size-selectivity curve (e.g., Challenger et al. 2017). However, it was not possible to estimate a size-selectivity curve, due to insufficient data, so juvenile captures were excluded from the analysis. While the data restriction was expected to minimize this issue, it is still possible that size selectivity still exists within the adult captures. Because the sample age structure is an important data input into the analysis, the reliability of the presented results therefore depends on the age structure of sampled adults reflecting the age structure of the adult population. If this assumption was not met the presented trends could be exacerbated. Currently there is no way to directly assess the accuracy of this assumption. Aging errors were another source of potential uncertainty but were expected to have a minimal impact on adult trends, which was the primary focus of the analysis. The lack of accurate aging, if significant, would have primarily affected the temporal accuracy of recruitment estimates, contributing to the general high level of uncertainty observed with this estimated component (i.e., Figure 11).

The adult Western Painted Turtle population in Revelstoke Reach was estimated to have undergone a statistically significant decline of approximately 29% from 2010 to 2017, conditional on sampling assumptions being met. The estimated decline appears to be largely linear with an average yearly decline of roughly 36 adult turtles per year (95% Credible Intervals [CI]: -49.7, -24.9 turtles per year). The coefficient of variation on the estimated trend was also large, around 17%; however, the effect size was large enough that the posterior mean was more than five standard deviations away. The results therefore suggest the possibility that the population has undergone decline within the study period. The trend was also



consistently estimated under different data subsets (i.e., Figure 7), indicating that it was likely not the by-product of different sampling methodologies applied within the study period. However, these results rely on the sampled adult age structure accurately reflecting the true age structure, which could not be directly assessed in this study. If smaller adults were significantly underrepresented in the sample this could have exacerbated the trend estimates. However, if the probability of capturing an adult turtle, regardless of size, was similar for all age (and size) classes, the results as presented may be plausible

Estimates of juvenile recruitment showed some potential evidence of a decline, although to a much lesser degree due to the high variability associated with estimating recruitment and trends in recruitment (i.e., the coefficient of variation for the recruitment trend was in excess of 100 per cent). Recruitment estimates in general will be more variable because information on recruitment is indirect. Only older Western Painted Turtles were included in this study (i.e., Females: Ages 5+; Males: Ages 9+), therefore information on recruitment comes from catch frequencies of older individuals and estimates of age specific mortality, which also showed high levels of uncertainty. As such, these estimates represent an extrapolation, which like all extrapolations, should be interpreted with caution. Furthermore, only a subset of years provided informative recruitment estimates (see the green shading in Figure 11). Uninformative years were associated with large uncertainty and mean estimates that were indistinguishable from the prior distribution (Figure 2). The earliest recruitment estimates would have been informed by captures of adults in the oldest age classes, of which there were only a few (Figure 3). While more recent uninformative recruitment years (i.e., grey shading Figure 11) resulted from the lag between turtles recruiting into the population and the time required for turtles to grow to a sufficient size such that they become exposed to the study's sampling methodology. This was especially evident for males, which featured a shallower growth curve (Figure 3) requiring more years to reach a sufficient size to enter the study's sampling program.

The estimated trends in recruitment may therefore be under represented, as informative years used for the estimates preceded the start of the study period and the study period featured a precipitous decline in some of the most productive female age classes (Figure 10). Population projections were based on first projecting recruitment trends forward from the informative recruitment years through the uninformative recruitment years during the study period (i.e., see Figure 12 and Figure 13) and then through the projection years. Recruitment projection Scenario 2 (doubling of the estimated recruitment trend) likely represents the most realistic scenario as the recent decline in reproductive females can be expected to have further exacerbate earlier recruitment declines estimated in informative years. Under Scenario 2, the rate of decline in the adult population continues with a projected population size of under 570 adults with 95% probability of the population being between ~200 and ~1300 by 2,057 (average recruitment trend: Figure 14b; sex-specific recruitment trend: Figure 15b). The total population trend was the same using either an average recruitment trend or sex-specific-specific trend, but sex-specific trends showed larger decline in males relative to females, which suggests that a female biased population could start to emerge within the next 40 years. However, if recruitment can be stabilized to recruitment levels estimated prior to the start of the study period it is feasible that the observed decline in the adult population can self-correct and stabilize (Figure 14c). If it does, the population will likely stabilize to a population size slightly larger than the start of the study period (i.e., approximately 950 reproductive adults, as compared to the start of the study period which was estimated to be approximately 890). This scenario also featured the largest uncertainty with a 95% probability of the population being between ~330 and ~2200 under this recruitment scenario, and as such a decline is still possible, but a low probability outcome.

All population projections featured a large degree of uncertainty that increased the further out the projection is taken. Uncertainty in population projections is an expected result of uncertainty in demographic parameters and plausible differences in study period demographics projections extended out



over time. While the highest fidelity can be expected within the study period, small differences in individual study period trajectories will result in expanding differences the further out the projection is taken. Projection uncertainty is therefore the consequence of multiple components including uncertainty in estimated recruitment, trends in recruitment, mortality at age and sampling rates compounded over time. Thus, projection precision can be increased by improving estimates of any of these components. Expanded sampling efforts to obtain age-at-known-size of turtles included in the study (both younger and older) would be one example of how this can be accomplished. Finally, the degree of uncertainty also differed time between scenarios; however, this was related to the increase in uncertainty over time exhibited by the associated recruitment scenarios. Recruitment scenarios that resulted in higher mean recruitment (e.g., Scenario 3 vs Scenario 2) also featured higher variability due to recruitment being log-normally distributed. As such, the only difference between the three population trajectories were the three recruitment scenarios used; all other types of uncertainty were the same between the three projection scenarios. Broader sampling of younger age classes (i.e., under 10 years) could help to improve precision of both recruitment estimates and projections and could be accommodated if the appropriate component, representing any methodological differences, was added to the model likelihood (e.g., see Abadi et al. 2010b).

The estimated decline in adult population within the study period, if true, may be the result of multiple factors acting directly and indirectly on turtle abundance or recruitment. The adult turtle population may have undergone a decline if recruitment rates cannot offset adult mortality rates. Although not part of the scope of this analysis, the influence of additive sources of turtle mortality on the population estimates is a significant source of uncertainty that warrants further investigation. For example, turtle populations are known to be sensitive to additive sources of adult mortality, particularly road mortality (Steen and Gibbs 2004), increased vegetation cover at nesting locations, which can result in more males entering the population (Janzen 1994; Refsinder and Janzen 2016), and predation by various species of wildlife (Hawkes 2017), all of which could be contributing to the observed decline in the turtle population.

The approach to modelling the Western Painted Turtle population in Revelstoke Reach provided a number of advantages over more classical modelling approaches to abundance estimation. The inclusion of an age structure population model (i.e., the VPA component) provides distinct advantages to more traditional Jolly-Seber type models, as estimates of the population size directly enters the likelihood rather being treated as a derived parameter (Schwarz 2001; Link and Barker 2005). This provides an avenue to include important constraints on population estimates. For example, if 15 older individuals (e.g., Age 25+) were first captured near the end of the experiment, these untagged individuals would have to also be alive at the start of the experiment given their age. The VPA component of the model thus ensures that these individuals are included in population estimates at the start of the assessment period. In contrast, a typical Jolly-Seber type abundance model cannot make use of such information, interpreting the new marks as recruitments from either recent births or immigration (i.e., recruits between the previous and current time step as well as a proportion occurring earlier but missed during sampling) based solely on estimated capture probabilities. As such, in Jolly-Seber type analyses it is not possible to use other available information to constrain population estimates (e.g., age-at-capture), rather population estimates rely on strong sampling assumptions and the accuracy of estimated capture probabilities. Estimates therefore will be much more sensitive to sampling assumptions (e.g., constant effect sampling area, full population mixing between sampling occasion, and equal capture probability of tagged and untagged individuals) than models that use auxiliary information such as age structure (e.g., Coggins et al. 2006) or spatial structuring (e.g., Schaub and Royle, 2014).

The current model did not distinguish between turtles that were only notched and those that were both notched and fitted with a radio-transmitter. The inclusion of telemetry units did not result in a known fate



experiment for these turtles, but rather increased the probability of detection, although realized capture frequencies were similar. The potential heterogeneity in detection rates would have affected the accuracy of absolute number of turtles, but appears to have had a minor impact on estimated population trends (e.g., see Figure 7). Rerunning the analysis using only notched turtles or only turtles fitted with radio-transmitters resulted in similar population trends. The robustness of trend estimates is not surprising given that integrated models tend to generally show less bias than non-integrated models due to the breadth of information included (Abadi et al. 2010a), and CJS based survival rates tend to be robust to detection heterogeneity (Pledger et al. 2003). The inclusion of turtles fit with radio-transmitters allowed for more precise age-specific mortality estimates which in-turned improved the precision of population projections. Without all available data (i.e., notched only and notch with radio-transmitter) population projections would have been too variable to provide any meaningful interpretation.

While estimates of trends appeared to be generally robust, the estimates of absolute numbers of adults were likely affected by the inclusion of turtles with radio-transmitters. Radio-transmitters can be expected to bias capture probabilities to values higher relative to notched only turtles. Unmarked turtles are captured with the same methodology as recaptures for turtles marked only with notches, therefore the size of the unmarked population was likely underestimated. As such, the absolute number of turtles in in Revelstoke Reach may be higher than what was estimated. Estimate of population trends, however, were found to be largely unaffected by the inclusion of turtles with radio transmitters. The similarity in results is likely due to the combination of constant proportional effort being applied to telemetry recoveries and the age-structuring included in the model. Together this likely allowed for reasonably robust estimates of trends despite the mixture of methodologies being used.

If more accurate estimates of numbers of turtles are required for management actions, the model will need to be extended to separately model recaptures of notched only turtles and turtles fitted with radio-transmitters. This can be achieved by including additional marked population matrices (Figure 1) for turtles marked with a transmitter in order to separately model the recaptures of turtles fitted with transmitters from turtles that were only notched. Estimated population trends are expected to remain largely unchanged, while the estimated abundance of adult turtles is expected to increase (i.e., a shift upwards of Figure 6a).

While the Revelstoke Reach Western Painted Turtle population is considered to be geographically closed (i.e., no immigration or emigration), the extent of the sampling area may have changed over time, with earlier study years (i.e., pre-2014) sampling a smaller subset of the population. If the age structure of the population is generally uniform over the geographic extent of the Revelstoke Reach population, then the age-structuring of the model would have largely mitigated the change in sampling area over time as new turtles encountered during the expanded geographical sampling coverage would have automatically been included in earlier years, thereby extending the effective sampling area of earlier study years.

The model also shared a number of components between sexes (i.e., mortality-at-age rates and yearly sampling rates which were used to derive capture probabilities), which could impact estimated population trends. Sex-specific trends could be biased if either males or females were undergoing differential population trends over the assessment period. For example, there were initial concerns that the population may have been male biased at the start of the assessment period (Basaraba 2014), but these concerns could not be confirmed due to the limited sampling. If a skewed sex ratio normalized during the assessment period (i.e., higher male mortality) this could have negatively biased female population trends. The model also assumed that males and females were equally catchable during the assessment period, which may not



always be the case (Tesche and Hodges 2015). If capture methodology resulted in sex-specific catchability differences that differentially changed over time, then this could also impact trend estimates. That said, a sensitivity analysis completed on a sub-set of data restricted to study years where sampling was carried out by LGL/ONA resulted in a similar trend estimates (Figure 7d), suggesting that if there were trends in sex-specific catchability differences that they were not related to later changes in field staff. Lastly, the model also assumed that age-structure did not differ spatially across the study area, if true population age-structure was not uniform across the geographical extent of the population, then estimated population trends could potentially be biased. Introducing a spatial component into the model (e.g., see Challenger et al. 2017) could provide a more direct test of this assumption, as well as refine estimates and understanding of population dynamics.

Refining the VPA component of the model to include sex-specific mortality rates, and potentially sex-specific sampling rates, could be useful. Female and male turtles grow at different rates; therefore, it is possible that age-specific mortality and capture rates also vary by sex. Improved aging estimates could allow the estimation of sex-specific mortality-at-age curves or the ability to model sex-specific mortality differences as a function of the difference in growth rates (e.g., Lorenzen 2000). While recapture probabilities for turtles captured using radio-telemetry are unlikely to be affected by turtle size, non-telemetry captures could be affected, which could result in different catchability for males and females. The impact of size on the ability for field gear (i.e., traps or capture methodology) to capture individuals is commonly considered in fisheries studies (e.g., Thompson 1994). Age or sized dependent capture selectivity could also be included in future revisions of the analysis model once more accurate growth curves are determined and there is a desire to included younger age classes (e.g., sub-adults or juveniles) in the analysis. The current analysis was restricted to adult turtles where age or size-specific capture differences are believed to be minimal.

Finally, data representing the younger age classes (i.e., under Age 10) would improve precision regarding age-specific mortality rates for those age classes, which in-turn would reduce uncertainty in recruitment estimates. Combining more precise age-specific mortality rates with refined growth curves (based on the inclusion of more carapace-at-known-age measurements) combined with expanded demographic sampling, would contribute to improved temporal accuracy of younger demographics such as recruitment. These improvements could then be used to assess the relationships between environmental variables and reservoir operations of the Revelstoke Reach Western Painted Turtle population.

Conclusions

This analysis provides a framework for assessing the status of the Western Painted Turtle population in Revelstoke Reach and some of the factors impacting it, but limited data on aging and data on other potentially confounding factors, such as road-based mortality, need to be quantified to further refine the population projections. Increased sampling targeting both the younger and older age classes, particularly males, could greatly improve the model outputs.

Model results indicate the potential for the adult Western Painted Turtle abundance in Revelstoke Reach to have undergone a significant and continuous decline since 2010. While coefficient of variation for the trend was large, about 17 to 20 per cent, the estimated trend was more than five standard deviations away from the mean, suggesting a potentially significant effect.

These results, while plausible, should be interpreted with caution given the limitations and assumptions associated with the current analysis model, as well as the fact the sampling program was not explicitly



designed to provide information trends in population abundances. A critical assumption therein was that the age structure of the sampled adults accurately reflected the adult age structure in the population. If this was not the case the estimated population trends may have been exacerbated. The estimated adult population decline within the study period, if true, may have also be the result of multiple factors acting directly and indirectly on turtle abundance or recruitment. For example, turtle populations are known to be sensitive to additive sources of adult mortality, particularly road mortality (Steen and Gibbs 2004), increased vegetation cover at nesting locations, which can result in more males entering the population (Janzen 1994; Refsinder and Janzen 2016), and predation by various species of wildlife (Hawkes 2017), all of which could be contributing to the observed decline in the turtle population. And although not assessed during the present study, previous work (e.g., Basaraba 2014) and Duncan (2016) found that the turtle populations in Revelstoke Reach will be experience potential, seasonal (and temporary) habitat displacement relative to changing reservoir levels but the overall impact of reservoir operations on turtles appears to be negligible.

The main limitations of the model are therefore related to 1) accurate aging of turtles; 2) age structure of the sampled adults accurately reflecting the true adult age structure in the population (i.e., no size selectivity within sampled adults); 3) different capture probabilities associated with notched vs. notched with radio transmitter; 4) lack of sex-specific mortality and sampling rate estimates; 5) the model did not consider the spatial distribution of turtles; and 6) population estimates were derived from studies not directly designed to support this goal. Aging accuracy, and by extension the age classes used in the model, could have affected the temporal accuracy of recruitment estimates and as such, temporal accuracy of recruitment estimates was unclear and therefore could not be used to assess management decisions. The accuracy of the estimated trends relies in part on the assumption of constant size selectivity within sampled adults, an assumption that could not be directly tested in the study. The mixture of tag types was also had an impact on the absolute estimate of abundance, but trend estimates were robust across different data subsets (e.g., all data, notched only, radio transmitter only, and 2014 to 2016 data only), suggesting that the estimated trends were largely insensitive to this issue. The sharing of yearly sampling rates and age-specific mortality rates could have impacted estimated population trends if these rates systematically differed by sex over the course of the study period. Similarly, the lack of a spatial structuring in the model could also have impacted trend estimates if sex- and age-specific systematically differed geographically across the study area. Due to the restricted sample size, the impact of sex- and spatial-specific differences were not directly assessed. Finally, the data used in this analysis comes from a series of field studies not directly designed to assess population trends. As such, it is unclear whether repurposing this data for the current analysis impacted estimated population trends.

The analysis undertaken cannot speak to causation of populations trends. However, following roughly 10 years of study, there are several possible factors that might be influencing the turtle population in Revelstoke Reach. These include road-based mortality of females during the nesting period, reduced habitat suitability at nesting sites (which occur outside of the drawdown zone), nest predation, and increased (although unmeasured) rates of predation on juveniles. Each of these factors could contribute directly and indirectly to the estimated trends reported herein. Previously completed work indicated that the turtle populations in Revelstoke Reach will experience potential, seasonal (and temporary) habitat displacement relative to changing reservoir levels but the overall impact of reservoir operations on turtles appears to be negligible. Without consideration of all variables that influence recruitment, mortality, and survival there will continue to be a larger degree of uncertainty associated with population trend projections.



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Appendix A: Capture Data

Table A1. Capture history data used in the analysis.

ID	Sex	Type ¹	Carapace (mm) ²	Age (years) ²	2010	2011	2012	2013	2014	2015	2016	2017
27	Male	N	164	21	0	0	0	0	0	0	1	0
F013	Female	N+T	191	13	1	0	0	0	0	0	0	0
F016	Female	N+T	203	17	0	0	0	0	1	1	0	0
F017	Female	N	192	13	1	1	0	0	0	0	0	0
F025	Female	N	203	17	1	1	0	0	0	0	0	0
F029	Female	N	185	12	0	1	0	0	0	0	0	0
F032	Female	N+T	195	14	1	1	0	0	0	0	0	0
F033	Female	N+T	213	23	0	0	0	0	0	0	1	0
F036	Female	N	216	27	0	1	0	0	0	0	0	0
F040	Female	N	204.5	17	0	1	0	0	0	0	0	0
F043	Female	N+T	192	13	0	1	0	0	0	0	1	1
F046	Female	N	192	13	0	1	0	0	0	0	0	0
F061	Female	N+T	120	5	1	1	1	0	1	0	0	0
F064	Female	N+T	182	11	1	1	1	0	0	0	0	0
F074	Female	N+T	183	12	1	1	0	0	0	0	0	0
F080	Female	N+T	183	12	0	1	0	0	0	0	0	0
F081	Female	N+T	154	8	0	1	0	0	0	0	0	0
F091	Female	N+T	197	15	0	1	1	0	0	0	0	0
F092	Female	N	152	7	0	1	0	0	0	0	0	0
F097	Female	N+T	195	14	0	1	0	0	0	0	0	0
F100	Female	N	192	13	0	1	0	0	0	0	0	0
F102	Female	N	188	12	0	1	0	0	0	0	0	0
F104	Female	N+T	152	7	0	1	0	0	0	0	0	0
F106	Female	N+T	187	12	0	1	1	0	0	0	0	0
F107	Female	N+T	201	16	0	1	1	0	0	0	0	0
F108	Female	N	185	12	0	1	0	0	0	0	0	0
F110	Female	N+T	196	14	0	1	0	0	0	0	0	0
F111	Female	N+T	187	12	0	1	1	0	0	0	0	0
F112	Female	N	165	9	0	1	0	0	0	0	0	0
F113	Female	N	211	21	0	1	0	0	0	0	0	0
F115	Female	N	199	15	0	1	0	0	0	0	0	0
F116	Female	N+T	182	11	0	1	1	0	0	0	0	0
F117	Female	N+T	172	10	0	1	1	0	0	0	0	0
F119	Female	N	189	13	0	1	0	0	0	0	0	0
F120	Female	N+T	180	11	0	1	1	0	0	0	0	0
F121	Female	N	181.5	11	0	1	0	0	0	0	0	0
F122	Female	N	195	14	0	1	0	0	0	0	0	0
F123	Female	N	185	12	0	1	0	0	0	0	0	0
F125	Female	N	147	7	0	1	0	0	0	0	0	0
F126	Female	N	210	20	0	1	0	0	0	0	0	0
F127	Female	N	203	17	0	1	0	0	0	0	0	0
F128	Female	N	201	16	0	1	0	0	0	0	0	0
F136	Female	N	167	9	0	1	0	0	0	0	0	0
F146	Female	N+T	147	7	0	0	1	0	1	0	0	0
F148	Female	N+T	195	14	0	0	1	1	1	0	1	0
F150	Female	N+T	185	12	0	0	1	0	0	0	1	0



ID	Sex	Type ¹	Carapace (mm) ²	Age (years) ²	2010	2011	2012	2013	2014	2015	2016	2017
F151	Female	N+T	207	19	0	0	1	1	0	0	0	0
F155	Female	N+T	205	18	0	0	1	0	0	0	0	0
F162	Female	N+T	201	16	0	0	0	1	0	0	0	0
F163	Female	N+T	201	16	0	0	0	1	0	0	0	0
F164	Female	N	179	11	0	0	0	1	0	0	0	0
F165	Female	N	206	18	0	0	0	1	0	0	0	0
F166	Female	N	180	11	0	0	0	1	0	0	0	0
F169	Female	N+T	207	19	0	0	0	1	0	0	0	0
F171	Female	N	199	15	0	0	0	1	0	0	0	0
F175	Female	N+T	188	12	0	0	0	1	0	0	0	0
F176	Female	N+T	141	6	0	0	0	1	1	0	0	0
F178	Female	N+T	159	8	0	0	0	1	1	0	0	0
F181	Female	N+T	155	8	0	0	0	1	1	0	0	0
F182	Female	N+T	187	12	0	0	0	1	1	0	0	0
F183	Female	N+T	176	10	0	0	0	0	0	0	1	1
F189	Female	N+T	204	17	0	0	0	0	1	0	0	0
F192	Female	N+T	189	13	0	0	0	0	1	0	0	0
F194	Female	N+T	194	14	0	0	0	0	1	0	0	0
F195	Female	N	200	16	0	0	0	0	1	0	0	0
F196	Female	N	202	16	0	0	0	0	1	0	0	0
F198	Female	N+T	202	16	0	0	0	0	1	0	1	0
F201	Female	N+T	220	40	0	0	0	0	1	0	0	0
F213	Female	N+T	216	27	0	0	0	0	0	0	1	1
F214	Female	N+T	193	14	0	0	0	0	0	1	0	0
F215	Female	N	181	11	0	0	0	0	0	1	0	0
F217	Female	N	143	7	0	0	0	0	0	1	0	0
F218	Female	N	159	8	0	0	0	0	0	1	1	0
F219	Female	N	186	12	0	0	0	0	0	1	0	0
F222	Female	N	164	9	0	0	0	0	0	1	0	0
F223	Female	N	149	7	0	0	0	0	0	1	0	0
F226	Female	N	154	8	0	0	0	0	0	1	0	0
F229	Female	N	176	10	0	0	0	0	0	1	0	0
F230	Female	N	187	12	0	0	0	0	0	1	0	0
F234	Female	N+T	191.5	13	0	0	0	0	0	1	1	1
F236	Female	N	176	10	0	0	0	0	0	1	0	0
F237	Female	N	143	7	0	0	0	0	0	1	0	0
F239	Female	N	179	11	0	0	0	0	0	1	0	0
F240	Female	N	195	14	0	0	0	0	0	1	0	0
F243	Female	N+T	208	19	0	0	0	0	0	1	1	1
F244	Female	N	203	17	0	0	0	0	0	1	0	0
F245	Female	N	177	10	0	0	0	0	0	1	0	0
F246	Female	N	203	17	0	0	0	0	0	1	0	0
F247	Female	N	213	23	0	0	0	0	0	1	0	0
F248	Female	N	193	14	0	0	0	0	0	1	1	0
F249	Female	N	217	28	0	0	0	0	0	1	0	0
F250	Female	N	171.5	10	0	0	0	0	0	1	0	0
F252	Female	N+T	131	6	0	0	0	0	0	0	1	0
F253	Female	N+T	207	19	0	0	0	0	0	0	1	1
F254	Female	N+T	161	8	0	0	0	0	0	0	1	1
F255	Female	N+T	199	15	0	0	0	0	0	0	1	0
F256	Female	N+T	158	8	0	0	0	0	0	0	1	1



ID	Sex	Type ¹	Carapace (mm) ²	Age (years) ²	2010	2011	2012	2013	2014	2015	2016	2017
F259	Female	N+T	148	7	0	0	0	0	0	0	1	0
F260	Female	N+T	191	13	0	0	0	0	0	0	0	1
F261	Female	N	190	13	0	0	0	0	0	0	1	0
F262	Female	N	200	16	0	0	0	0	0	0	1	0
F264	Female	N	191	13	0	0	0	0	0	0	1	0
F267	Female	N	178	11	0	0	0	0	0	0	1	1
F271	Female	N	146	7	0	0	0	0	0	0	1	0
F272	Female	N	208	19	0	0	0	0	0	0	1	0
F273	Female	N	158	8	0	0	0	0	0	0	1	0
F274	Female	N	165	9	0	0	0	0	0	0	1	0
F277	Female	N	194	14	0	0	0	0	0	0	1	0
F278	Female	N	178	11	0	0	0	0	0	0	1	0
M035	Male	N	146	16	0	0	0	0	0	1	0	0
M048	Male	N	170	24	0	0	0	0	1	0	0	0
M053	Male	N	137	15	0	0	0	0	0	1	0	0
M082	Male	N+T	132	14	0	1	0	0	0	0	0	0
M084	Male	N+T	177.5	27	0	1	1	0	0	0	0	0
M086	Male	N+T	155	19	0	1	1	0	0	0	0	0
M087	Male	N+T	180	28	0	1	1	0	0	0	0	0
M088	Male	N+T	170.5	24	0	1	1	0	0	0	0	0
M090	Male	N+T	161	20	0	1	1	0	0	0	0	0
M093	Male	N	133	14	0	1	0	0	0	0	0	0
M094	Male	N	160	20	0	1	0	0	1	0	0	0
M098	Male	N+T	167	22	0	1	0	0	0	0	0	0
M099	Male	N+T	172	24	0	1	1	0	0	0	0	0
M109	Male	N	169	23	0	1	0	0	0	0	0	0
M132	Male	N+T	123	12	0	1	0	0	0	0	0	0
M145	Male	N	146	16	0	0	1	0	0	0	0	0
M147	Male	N+T	143	16	0	0	1	0	0	0	0	0
M149	Male	N+T	124	12	0	0	1	1	0	0	0	0
M152	Male	N+T	125	12	0	0	1	0	0	0	0	0
M153	Male	N+T	160	20	0	0	1	0	0	0	0	0
M154	Male	N+T	124.5	12	0	0	1	0	0	0	0	0
M157	Male	N+T	161	20	0	0	0	1	1	0	0	0
M158	Male	N+T	143	16	0	0	0	1	0	0	0	0
M159	Male	N+T	169	23	0	0	0	1	0	0	0	0
M160	Male	N+T	179	28	0	0	0	1	1	0	0	0
M161	Male	N+T	171	24	0	0	0	1	0	0	0	0
M167	Male	N+T	179	28	0	0	0	1	1	0	0	0
M170	Male	N	159	20	0	0	0	1	0	0	0	0
M172	Male	N	186	32	0	0	0	1	1	1	1	0
M174	Male	N+T	125	12	0	0	0	1	1	0	0	0
M177	Male	N+T	161	20	0	0	0	1	1	0	0	0
M179	Male	N+T	168	23	0	0	0	1	0	0	0	0
M180	Male	N+T	127.5	13	0	0	0	1	0	0	0	0
M184	Male	N+T	163	21	0	0	0	1	1	0	0	0
M185	Male	N	145	16	0	0	0	0	1	0	0	0
M186	Male	N	167.5	23	0	0	0	0	1	1	0	1
M187	Male	N	157	19	0	0	0	0	1	1	0	0
M189	Male	N	163	21	0	0	0	0	1	0	0	0
M190	Male	N	124	12	0	0	0	0	1	0	0	0



ID	Sex	Type ¹	Carapace (mm) ²	Age (years) ²	2010	2011	2012	2013	2014	2015	2016	2017
M193	Male	N	172	24	0	0	0	0	1	0	0	1
M195	Male	N	138	15	0	0	0	0	1	0	0	0
M197	Male	N	174	25	0	0	0	0	1	0	0	0
M199	Male	N	120	11	0	0	0	0	1	0	0	0
M200	Male	N	189	34	0	0	0	0	1	0	0	0
M201	Male	N	168	23	0	0	0	0	1	0	0	0
M202	Male	N	171	24	0	0	0	0	1	0	0	0
M203	Male	N	187	33	0	0	0	0	1	0	0	0
M203a	Male	N	170	24	0	0	0	0	0	0	1	0
M204	Male	N	171	24	0	0	0	0	1	0	0	0
M205	Male	N	156	19	0	0	0	0	1	0	0	0
M206	Male	N	151	18	0	0	0	0	1	0	0	0
M207	Male	N	173	25	0	0	0	0	1	1	0	0
M208	Male	N	174	25	0	0	0	0	1	0	0	0
M209	Male	N	189	34	0	0	0	0	1	0	0	0
M210	Male	N	137	15	0	0	0	0	1	0	0	0
M211	Male	N	128	13	0	0	0	0	1	1	0	0
M212	Male	N	125	12	0	0	0	0	1	0	0	0
M216	Male	N	172	24	0	0	0	0	0	1	0	0
M220	Male	N	162	21	0	0	0	0	0	1	0	0
M221	Male	N	165	22	0	0	0	0	0	1	0	0
M224	Male	N	174	25	0	0	0	0	0	1	0	0
M225	Male	N	158	20	0	0	0	0	0	1	0	0
M227	Male	N	168	23	0	0	0	0	0	1	0	0
M228	Male	N	152	18	0	0	0	0	0	1	0	0
M229	Male	N	167	22	0	0	0	0	0	1	0	0
M231	Male	N	163	21	0	0	0	0	0	1	0	0
M232	Male	N	159	20	0	0	0	0	0	1	1	0
M233	Male	N	159	20	0	0	0	0	0	1	1	0
M235	Male	N	160	20	0	0	0	0	0	1	1	0
M238	Male	N	166	22	0	0	0	0	0	1	0	0
M241	Male	N	137	15	0	0	0	0	0	1	0	0
M242	Male	N	153	18	0	0	0	0	0	1	0	0
M251	Male	N	183	30	0	0	0	0	0	1	1	0
M257	Male	N	162	21	0	0	0	0	0	0	1	0
M258	Male	N	166	22	0	0	0	0	0	0	1	0
M263	Male	N	161	20	0	0	0	0	0	0	1	0
M265	Male	N	148	17	0	0	0	0	0	0	1	0
M266	Male	N	164	21	0	0	0	0	0	0	1	0
M268	Male	N	147	17	0	0	0	0	0	0	1	0
M269	Male	N	174	25	0	0	0	0	0	0	1	0
M270	Male	N	150	17	0	0	0	0	0	0	1	0
M275	Male	N	151	18	0	0	0	0	0	0	1	0
M276	Male	N	130	13	0	0	0	0	0	0	1	0
M279	Male	N	183	30	0	0	0	0	0	0	1	0
M280	Female	N	174	10	0	0	0	0	0	0	1	0
M281	Male	N	173	25	0	0	0	0	0	0	1	0
M282	Male	N	125	12	0	0	0	0	0	0	1	0
M283	Male	N	135	14	0	0	0	0	0	0	1	0
T114	Female	N+T	161	8	0	1	0	0	0	0	0	0
T3	Male	N	167	22	0	0	0	0	0	0	1	0



ID	Sex	Type ¹	Carapace (mm) ²	Age (years) ²	2010	2011	2012	2013	2014	2015	2016	2017
T41	Male	N	170	24	0	0	0	0	0	0	1	0
T45	Male	N	157	19	0	0	0	0	0	0	1	0

¹ Type indicates whether notch only (N) or notch plus transmitter (N+T) were applied.

² Carapace length and associated ages are for first capture occasion.

