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Spawning distribution and abundance of a northern Chinook salmon population

S. A. SETHI & T. TANNER

US Fish and Wildlife Service, Anchorage, AK, USA

Abstract Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), is an important biological and cultural resource in Alaska, but knowledge about Chinook salmon ecology is limited in many regions. From 2009 to 2012, spawning distribution and abundance of a northern Chinook salmon population on the Togiak River in south-west Alaska were assessed. Chinook salmon preferred deeper mainstem channel spawning habitat, with 12% (14 of 118 tags in 2009) to 21% (22 of 106 tags in 2012) of radio-tagged fish spawning in smaller order tributaries. Tributary spawners tended to have earlier run timing than mainstem spawners. Chinook salmon exhibited extended holding and backout (entering freshwater but returning to saltwater before completing anadromous migration) behaviours near the mouth of Togiak River, potentially prolonging their exposure to fishery harvest. Mark–recapture total annual run estimates (2010–2012) ranged from 11 240 (2011) to 18 299 (2012) fish. Exploitation of Chinook salmon ranged from 36% (2012) to 55% (2011) during the study period, with incidental fishery catches near the mouth of the river comprising the largest source of harvest.

KEYWORDS: Alaska, fish movement, fisheries management, mark–recapture, *Oncorhynchus tshawytscha*, run timing.

Introduction

Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), is a critical component of commercial, sport and subsistence fisheries in Alaska, USA. Recently, Chinook salmon abundance has declined across multiple Alaskan stocks, resulting in closures of commercial and subsistence fisheries in the Yukon and Kuskokwim rivers in 2011 and 2012, and Upper Cook Inlet streams in 2012. These closures lead to a fishery disaster declaration for areas of the State of Alaska during 2012 (Blank 2012). Multiple hypotheses have been put forward to explain the drivers of recent Chinook salmon dynamics across the State, including changes in mortality during freshwater juvenile life history stages, increases in ocean mortality and pathogens during the spawning migration *inter alia* (Schindler *et al.* 2013); however, understanding of basic Chinook salmon ecology is lacking in many regions.

Bristol Bay in south-west Alaska (Fig. 1) supports a large Chinook salmon complex (Fair *et al.* 2012), and, behind the Nushagak River, the Togiak River run provides the second largest harvests of Chinook salmon in Bristol Bay for both sport (Dye & Schawnke 2012) and commercial fisheries (Sands 2012). The Togiak River Chinook salmon population is unique, representing a small-watershed salmon system in south-western and western Alaska. The Togiak River has a considerable Chinook salmon run for its size (see below). Two nearby villages of Togiak and Twin Hills rely substantially on Togiak River salmon for both commercial revenues and subsistence harvest.

The Togiak Chinook salmon run has traditionally been managed under fixed escapement goals based on aerial surveys conducted by the Alaska Department of Fish and Game (ADFG; Baker *et al.* 2009), where total escapement was reconstructed by expanding visual aerial counts with correction factors (Bue *et al.* 1998). The most recent aerial escapement survey was flown in 2005 (Salomone *et al.* 2009), and high monitoring costs have precluded additional surveys since that time (Fair *et al.* 2012). Aerial surveys indicated spawning aggregations were concentrated within the upper mainstem river and spread across tributary habitats; however, turbidity and water depth presented difficulties in detecting spawning aggregations in lower mainstem habitat. Additionally, surveys were typically flown only once per year, providing a snapshot of the spawning migration. Presently,

Correspondence: Suresh A. Sethi, U.S. Fish and Wildlife Service, Fisheries and Ecological Services, Anchorage, AK, USA (e-mail: suresh_sethi@fws.gov)

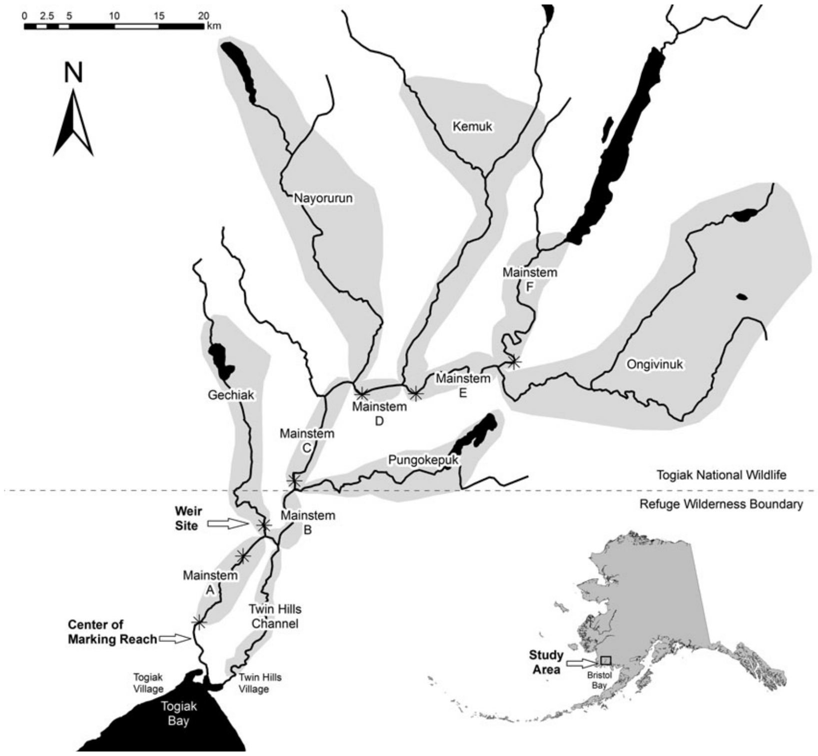

Figure 1. Togiak River study area. Spawning enclaves (shaded grey polygons) correspond to the Alaska Department of Fish and Game aerial survey delineations (Brookover *et al.* 1996). Fish tagging occurred in the lowest reach of the mainstem river; the weir on Gechiak Creek was the primary recapture site for the mark–recapture abundance study. Fixed radio telemetry stations are indicated with asterisks. Togiak Bay at the mouth of the river is saltwater habitat.

there is a lack of basic information related to the spawning ecology or status of the stock, and subsistence, sport and commercial harvest demands are expected to continue (Clark 2009). Prior to this study, estimates of escapement have been based on aerial indices, and no direct estimate of escapement for management purposes has been available.

This article reports results from a 4-year study of Togiak Chinook salmon from 2009 to 2012 that was developed to help inform current and future management of the stock. Information is provided on the spawning distribution, movement and run timing behaviour, abundance and exploitation rates observed over the study period. A combination of mark–recapture analyses and radio telemetry was used to address the following objectives: (i) assess the spawning distribution of Chinook salmon within the Togiak River drainage; (ii) estimate in-river run timing; (iii) estimate escapement of Togiak River Chinook salmon using a closed population mark–recapture design; and (iv) using information on reported harvests, reconstruct subsistence, sport and commercial exploitation rates. Analyses include several features of interest for assessing salmon populations using tagging data including mark–recapture bias simulation modelling and a Bayesian implementation of a parametric run timing model. R code (R Development Core Team 2013) to replicate modelling analyses is included as online Supplementary Information.

Methods

Study area

The Togiak River is located in south-west Alaska and lies within the Togiak National Wildlife Refuge (Fig. 1). The watershed encompasses 5178 km², includes nine major lakes and five major tributaries and is bounded on the east by the Wood River Mountains and on the west by the Ahklun Mountains. The Togiak River originates at the outlet of Togiak Lake and flows 93 river kilometres (rkms) to saltwater at Togiak Bay. Climate in the Togiak River watershed ranges from subarctic maritime near the Bristol Bay coast to subarctic continental moving towards the interior headwaters of the river. The Togiak River system is complex; smaller tributaries have more gravel and cobble substrate and generally are clear, whereas the mainstem channel has patches of gravel and cobble and gravel bars and is more turbid. The watershed upstream of the confluence with Pungokepuk Creek is part of a U.S. congressionally designated Wilderness Area (USFWS 1990).

Tagging efforts

During 2009–2012, adult Chinook salmon returning to spawn in the Togiak River drainage were captured using a drift gillnet (18.3-m-long, 4.6-m-deep, 20.3-cm-stretched mesh size) deployed from a skiff in the lower 5 km of the mainstem river (Fig. 1). In 2011 and 2012, additional tagging effort was applied using hook-and-line sampling with artificial lures. The tagging area was sited in a mainstem reach below the lowest spawning enclave corresponding to historical aerial abundance survey river segments used by the ADFG (Brookover *et al.* 1996); telemetry tracking during this study (see below) confirmed radio-tagged fish were not observed spawning downstream of the tagging site. During gillnet fishing, the net was removed from the water and fish were handled after every strike to reduce handling time and mortality of sampled fish. In all years, capture effort was dispersed throughout the tagging section along both banks of the river.

Two types of tags were implanted into salmon: Model No. F1840B radio tags (Advanced Telemetry Systems Incorporated®, Isanti, MN, USA) and 30.5-cm serially numbered model FT-4 Floy® spaghetti tags (Seattle, WA, USA). Radio tags were implanted into healthy fish greater than 450 mm in length (mid-eye to tail fork). All radio-tagged fish also received a spaghetti tag. Radio tags consisted of a transmitter encapsulated in a biologically inert polypropylene co-polymer and equipped with a stainless steel, nylon-coated whip antenna. Radio tags weighed 22 g, which never exceeded 2% of the fish's body weight (Winter 1983) and were implanted through the oesophagus using a plunger as described by Burger *et al.* (1985). Radio tags included a mortality signal, which was activated after a tag remained stationary for 8 h or longer. Field observations indicated that fish were healthy at the time of release after tagging and were not substantially affected through the radio-tagging process. Furthermore, tag regurgitation and mortality signals during the study were rare, with suspected pre-spawn natural mortality and/or tag regurgitation rates of 3.1, 2.3, 3.8 and 5.7% in 2009, 2010, 2011 and 2012, respectively (percentage of all successfully fated tags in a given year; data in Table 1).

Tagging efforts in 2009–2010 were based on a schedule of a prescribed fixed number of radio tag releases per temporal release stratum to ensure fish throughout the run were radio-tagged for subsequent spawning location tracking. During these years, gillnetting occurred daily until the tag quota was reached or the stratum ended (Table S1). Tagging efforts in 2011–2012 were standardised to achieve tagging rates in proportion to abundance as fish entered the river, applying 2.0 h of soak time for drift gillnetting and 1.0 h of hook-and-line fishing with two lines in the water per day throughout the tagging season. In 2011–2012, a target quota of radio tags was allocated per stratum, but spaghetti tags were deployed into all captured healthy fish, regardless of size and whether they received a radio tag. During 2011–2012, gillnetting and line fishing occurred 6 days per week throughout the tagging period (Table S1).

Table 1. Fates of radio-tagged Chinook salmon entering the Togiak River, 2009–2012

	2009	2010	2011	2012
Spawned	118	160	113	106
Harvested	7	22	41	24
Natural mortality and regurgitation	4	6	6	8
Unknown fate	25	23	11	9
Total	154	211	171	147

Spawning location and movement tracking

A combination of aerial and small-boat surveys and fixed receiver stations were used to locate salmon marked with radio tags. Aerial surveys were conducted from a fixed-wing aircraft equipped with an H-antenna mounted on each wing strut and flown approximately 100–400 m above the ground approximately once every 2 weeks throughout each study season. Small-boat surveys were conducted approximately 5 days a week in open skiffs using a 4-element Yagi antenna (Advanced Telemetry Systems). Additional detections were obtained through a network of seven fixed receiver stations (Fig. 1). Surveys and fixed stations used Advanced Telemetry Systems model R4500C or R4520C receiver–dataloggers containing on-board GPS units. Four to six aerial surveys and 29–42 boat surveys were conducted throughout the July–September telemetry tracking periods for each field season (Table S1).

Radio-tagged fish were assigned one of four fates: spawning, harvested, non-harvest mortality or tag regurgitation and unknown (Table 1). Radio-tagged fish were considered spawning when a tagged fish was either observed exhibiting spawning behaviour (redd digging, staging in spawning pairs or aggregations or actively spawning) or when multiple successive detections of a tag in the same location occurred during periods of known spawning activity (generally August and early September) and for which the fish was known to be alive as confirmed visually or as inferred by its movement behaviour through radio tag detections. Harvested tags were returned by fishers. Non-harvest mortality (e.g. senescence-related death, tagging-related death and bear predation) and tag regurgitation were identified when a located tag was found emitting a mortality signal. Fish whose spawning location was successfully identified were assigned to spawning enclaves as defined by sections A–F for the mainstem river, corresponding to historical aerial abundance survey river segments used by the ADFG (Brookover *et al.* 1996), or to one of five tributary rivers as defined by ADFG aerial surveys with the addition of the Twin Hills Channel as a sixth tributary (Fig. 1).

Movement included milling (i.e. holding), migration and backout behaviour (see below) and was assessed using information collected between time of tagging and subsequent detections via mobile tracking or fixed receiver stations. Between 2010 and 2012, it was possible to assess whether returning Chinook salmon entered the river and held for a period of time or moved steadily towards their ultimate spawning location. A fish was considered to exhibit holding behaviour if it was detected milling in the lower river in a localised region for one or more days before ultimately being fated as spawning in a different location. Due to difficulty in differentiating spawning versus milling behaviour for lower-river spawning fish, mainstem-A spawning-fated fish were excluded from holding behaviour calculations. It was not possible to reliably construct holding behaviour during 2009 due to limitations in tracking data. Backout behaviour occurs when returning salmon enter freshwater spawning habitat but then subsequently move back into saltwater. Backouts were detected with opportunistic aerial telemetry surveys over Togiak Bay and through tag returns from commercial fishers operating in Togiak Bay (Fig. 1).

Recapture sampling for abundance estimation

During 2010–2012, recapture sampling for abundance estimation was conducted at a resistance board weir installed on Gechiak Creek 2 rkm from the confluence with the mainstem river (Fig. 1; Table S1). The weir was fitted with a closable fish passage chute that allowed fish to pass into a live trap to facilitate identification of salmon to species and enumeration of all unmarked and marked Chinook salmon. The weir was manned during daylight hours each day ($\sim$600–2400 Alaska daylight savings time), and the fish passage chute was closed during unmanned hours to prevent fish from passing the weir. During extreme high-water days (typically <7 days/field season), the weir was deemed unsafe to operate and the fish passage chute was fixed open allowing fish to pass without being enumerated; hence, weir counts represent a partial count of the total Gechiak Creek run.

In addition to weir recapture sampling, carcass surveys were conducted in spawning areas of the upper tributaries of the Togiak River drainage during the 2012 field season in an attempt to increase tag recaptures (Table S1). Field crews randomly chose spawning locations accessible by boat and enumerated both marked and unmarked Chinook salmon carcasses. To prevent bias of carcass survey locations towards areas where radio-tagged fish were known to reside, crewmembers choosing carcass survey locations were excluded from participation in radio-tracking surveys. Marked fish were identified by the presence of a Floy tag. The tails of counted carcasses were cut off to prevent double counting by observers.

Run timing

Run timing curves were fit to observed catch-per-unit-effort data (Chinook salmon per h of drift gillnetting soak time) from the tag release site in 2009–2012. The shape of the run timing curve was described with a normal distribution curve, and deviations between observed and predicted run timing cumulative proportions were modelled as normally distributed. The model was fit in a Bayesian framework using WinBUGS (Lunn *et al.* 2000) as run from R2WinBUGS (Sturtz *et al.* 2005). Model code is presented in Data S1.

The count of tags ultimately fated to tributary or mainstem spawning locations that were deployed during the respective temporal release strata was used as an index of run timing at the tagging site with which to test for run timing differences between mainstem and tributary spawners within study years. Differences in counts of tags released were tested using a Fisher's exact test (Zar 2010). Under the null hypothesis of no difference in run timing at the tagging site, all spawning enclaves would have the same proportion of tags released in a given release stratum.

In-river abundance estimation

In-river abundance of adult returning salmon that escaped the commercial fishery was estimated using the Lincoln–Petersen closed population estimator (Seber 2002) implemented in a Bayesian framework using WinBUGS and R2WinBUGS. Tag release and tag recovery data were generated following field efforts outlined above. Briefly, spaghetti tags served as the visual mark for the abundance estimation mark–recapture portion of this study. Tag releases encompassed the radio- and spaghetti-tagging sampling efforts outlined above, and recapture sampling occurred at the Gechicak Creek weir and through opportunistic carcass surveys in tributary spawning grounds. Subsistence and sport harvests were minimal below the tagging reach, and thus, in-river abundance was defined as run size at the tagging reach; total run size was defined as in-river abundance plus commercial harvest that occurred in Togiak Bay (see below). Code for the WinBUGS model is provided in Data S2. The assumptions of the Lincoln–Petersen model are: (1) the population is closed to additions or deletions; (2) marks are not lost or misidentified and (3) all animals are equally likely to be captured during tagging or recapture sampling (Pollock *et al.* 1990; Seber 2002). Additions to the population were non-existent because all fish in the study had to pass the tagging site. Efforts were made to avoid tagging-related mortality by deploying tags only into healthy fish, and it was assumed that any mortality events (e.g. sport harvest) were randomly distributed throughout the tagged and untagged population. As a result, it is believed that assumption 1 is valid and that the estimator provides an assessment of abundance at the tagging site (Krebs 1999). The brightly coloured spaghetti tags were readily identified through the recapture sampling at the weir and during carcass surveys. Spaghetti tags were passed through the tough dorsal tissue of salmon, and tag losses were assumed to be negligible. Thus, it is believed assumption 2 is valid.

Tagging efforts during the 2011 and 2012 season were standardised across tagging days, ensuring that spaghetti tag releases occurred in proportion to abundance and satisfying assumption three that all animals were at equal risk of capture during the tagging event. Note that by maintaining equal probability of capture at the time of tagging for all individuals in the population, the systematic recapture event at Gechiak Creek weir maintains the relative proportions of tagged and untagged animals in the systematic subsample as in the overall population, leading to valid abundance estimation. (Also see simulation analyses in Data S3 that demonstrates that this design leads to unbiased abundance estimation.) By contrast, assumption 3 was potentially violated during 2010 sampling because tagging effort was not standardised across days but was implemented such that a set number of tags during each release stratum was deployed (see above). Field crews implemented more tagging effort during the tails of the Chinook salmon run as opposed to release strata during the peak of the run in an attempt to satisfy tag release targets in this study year. Because the recapture sample in this study during 2010 represented a systematic sample of fish bound for Gechiak Creek, this design could introduce capture heterogeneity into the data, whereby fish entering the tagging site along a bell-shaped run curve may receive different tag rates through the population if tag release numbers were held constant across time. For example, tagging data suggest that tributary-bound fish such as the Gechiak Creek subpopulation tended to have earlier run timing into Togiak River than mainstem spawners (see Results: *Run timing,* below). In this case, the tributary fish would be at risk of receiving a greater tag rate than mainstem fish, which enter in larger numbers later in the run. Because the recapture sample was on a tributary weir, the recapture tag rate could be inflated, biasing total abundance low.

To assess whether this form of capture heterogeneity may have resulted in abundance estimation bias for the 2010 field season, simulation analyses were conducted to model the direction and potential magnitude of bias expected when a tributary run arrives in advance of the rest-of-run stock complex using a schedule of tag releases, recapture rates, tributary escapement levels (observed at the Gechiak Creek weir) and a total stock size based on data from the 2011 to 2012 seasons. Simulation results suggest that the 2010 abundance estimate was biased low by potentially 25% (relative to the true value); to accommodate this, abundance and exploitation estimates are presented below for 2010 with and without a correction for bias possibly induced by the 2010 tagging protocol. The estimate of mean bias and associated spread about the expected bias from simulations outlined in Data S3 were incorporated into the Bayesian implementation of the mark–recapture model by calculating bias-adjusted total run size as a derived parameter (Data S2). The bias simulation model and full results are presented in Data S3.

Exploitation rates

ADFG publishes annual estimates of commercial ($C_{C,t}$), subsistence ($C_{P,t}$) and sport harvest ($C_{S,t}$; reproduced in Table S2). Commercial harvest information comes from ADFG fish ticket data for the Togiak Bay fishing district and constitutes incidental Chinook salmon catch during a directed sockeye salmon, *O. nerka* (Walbaum), fishery; sport and subsistence Chinook salmon harvest occur in fresh water predominately in the lower mainstem river. Sport harvest on Togiak River is comprised almost exclusively of guided angler catches and is reported by licensed guides through required logbook mail-in surveys. Subsistence harvest is estimated from voluntary surveys mailed to residents of the Togiak district (Dye & Schawnke 2012). Survey-based sport and subsistence harvest data require self-reporting and contain error in reconstructing riverwide harvests, but validation analyses by ADFG suggest that systematic bias between survey-based harvests and actual harvests is not prevalent (Clark 2009).

Commercial harvest occurs in Togiak Bay outside of the Togiak River, whereas subsistence and sport harvests occur predominately in-river. Measures of annual harvest rate ($H_{C,t}$, $H_{P,t}$ and $H_{S,t}$) were included as derived parameters in the Bayesian implementation of the Lincoln–Petersen estimator, taking into account the order of harvests (Data S2). ADFG does not publish uncertainty estimates of harvest numbers, so posterior distributions for harvest rates assume catches are reported without observation error.

Results

Spawning distribution

Mainstem spawners comprised the majority of radio-tagged fish between 2009 and 2012 (Table 2). Assuming tagged fish represented a random sample from all spawning fish, on average 84.9% (range: 79.2–88.1%) of Togiak Chinook salmon spawn in mainstem reaches. The proportion of tags fated to different spawning enclaves varied year to year, but no tributary was observed to receive more than 7.5% of the total number of fish successfully fated to spawning locations in a given year.

Table 2. Spawning distribution of radio-tagged Chinook salmon in Togiak River, 2009–2012. Reported tag numbers and percentages reflect successfully fated radio tags

	2009		2010		2011		2012	
River section	Tags	%	Tags	%	Tags	%	Tags	%
Mainstem								
Section A	35	29.7	15	9.4	22	19.5	13	12.3
Section B	14	11.9	18	11.3	20	17.7	19	17.9
Section C	22	18.6	26	16.3	23	20.4	26	24.5
Section D	7	5.9	13	8.1	13	11.5	12	11.3
Section E	18	15.3	28	17.5	13	11.5	7	6.6
Section F	8	6.8	28	17.5	8	7.1	7	6.6
Subtotal	104	88.1	128	80.0	99	87.6	84	79.2
Tributaries								
Gechiak Creek	6	5.1	9	5.6	4	3.5	2	1.9
Pungokepuk Creek	3	2.5	8	5.0	1	0.9	2	1.9
Nayorurun River	3	2.5	6	3.8	2	1.8	8	7.5
Kemuk River	2	1.7	4	2.5	1	0.9	5	4.7
Ongivinuk River	0	0.0	3	1.9	6	5.3	5	4.7
Twin Hills Channel	–	–	2	1.3	0	0.0	0	0.0
Subtotal	14	11.9	32	20.0	14	12.4	22	20.8
Total tags fated	118		160		113		106	
Total tags released	154		211		171		147	

Run timing

Catch-per-unit-effort data at the tagging site yielded precise run timing curve fits. Peak run times varied across the study by only a few days, with the earliest peak in 2009 at Julian date 193 (rounded to the nearest day; Gregorian calendar day 12 July 2009) and the latest run peak estimated at Julian date 197 in 2011 (16 July 2011; Fig. 2). The compression of the run timing curves, measured by the fitted normal run curve spread parameter (σ), varied more substantially over the study period. In 2009, the most compressed run, the middle 90% of the run was estimated to take 23.4 days to pass the tagging site (calculated based upon the posterior mean of estimated run spread parameters), whereas in 2012, the most diffuse run, the middle 90% of the run, was estimated to take 14 days longer to pass the tagging site (37.5 days).

Pooling across tributary-bound fish, information on fated tags dated back to release strata suggests that tributary fish as a group tended to have earlier run timing than mainstem fish for all years except 2009 (Fisher's exact tests against the null of no difference in tag release timings across strata for tributary versus mainstem fish: 2009, $P = 0.841$; 2010, $P = 0.024$; 2011, $P = 0.025$; 2012, $P = 0.008$; Table 3). Tag releases by strata indicated that the difference in peak run timing between tributary- and mainstem-bound fish was generally one temporal stratum or less and was greatest in 2010 (Table 3). Furthermore, tributary runs appeared to be more compressed than the larger, combined mainstem run (Table 3). In all but two cases, no statistically significant difference in run timing was identified amongst individual tributary spawning substocks or amongst mainstem spawning substocks within any of the study years. The two exceptions were in 2011 when mainstem river section A appeared to have later run timing than any of the other mainstem sections (Fisher's exact test, $P = 0.004$) and in 2012 when Nayorurun River appeared to have earlier run timing than any of the other tributary rivers (Fisher's exact test, $P = 0.041$; run timing data for specific tributaries are not shown but are available from the authors upon request). It is cautioned, however, that tag release timing data for specific substocks as determined by fating radio tags to spawning enclaves were sparse, resulting in very few or zero tag releases in some strata for a number of subpopulations. As a result, tests

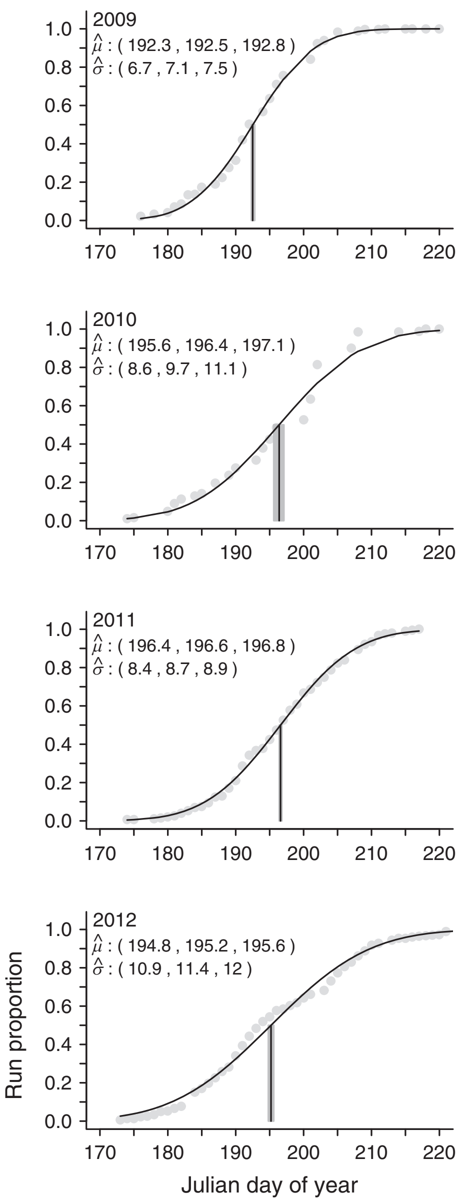

Figure 2. Cumulative run timing curves 2009–2012. Grey dots are the observed proportion of cumulative catch-per-unit-effort by Julian day of year, and the curve is the model fit. Vertical grey polygons and black lines represent the posterior mean and the 95% credibility interval for the peak run day under the assumption of a Normal distribution shaped run curve; grey polygons are narrow in some instances, reflecting high precision in peak run day estimates. Posterior means and 95% credibility intervals (lower interval limit, posterior mean, upper interval limit) are also displayed in text for the mean (μ) and spread (σ) parameters of the fitted underlying Normal curves that describe the salmon run progression (see Data S1). For reference, Julian day 195 = Gregorian calendar day July 14 during non-leap years.

of independence such as the Fisher's exact test may have low power to detect differences in run timing for specific substocks (e.g. Zar 2010).

Holding behaviour and backouts

Returning Chinook salmon typically held in the lower reaches of the mainstem Togiak River and above the tagging site (mainstem section A; Fig. 1) for 2 weeks or longer, with some fish holding as long as 40 days before moving further upstream for spawning (Table 4). Differences in holding behaviour were statistically significant amongst years (one-way ANOVA, $F_{2,319} = 3.11$, $P = 0.045$) and between mainstem versus tributary spawners (*t*-test, $t_{320} = 2.60$, $P = 0.009$); however, the difference in mean holding days across groups was typically 7 days or less, and no clear pattern emerged across time or spawning distribution.

In addition to holding behaviour, evidence was found of fish backing out into saltwater after moving into lower mainstem reaches through tag reporting by commercial fishers and opportunistic aerial surveys that covered the lower mainstem and the saltwater Togiak Bay near the mouth of the Togiak River. Due to limited aerial tracking in the saltwater habitat of Togiak Bay, it was only possible to confirm 10 radio-tagged fish that backed out into saltwater after entering Togiak River during 2010–2012. Of these, three fish returned to successfully spawn and seven were harvested in the commercial drift gillnet fishery in Togiak Bay.

Abundance and exploitation rates

Using the unadjusted abundance estimate for 2010, the 3-year average total run size (escapement + commercial harvest + sport harvest + subsistence harvest) for Togiak Chinook salmon was 14 972 fish (16 986 fish with the bias-adjusted 2010 estimate; Table 5). Total harvest amount remained stable across the study years, but run size in 2011 was considerably lower than in 2010 or 2012. As a result, the total exploitation rate varied from 36 to 55%, with incidental commercial take from the directed Sockeye salmon fishery comprising the largest source of exploitation, followed by subsistence use and sport harvest.

Discussion

While numerically smaller than some western and south-western Alaskan stocks, the Togiak Chinook salmon population is an important component in the regional Chinook salmon stock complex, potentially contributing to Chinook salmon life history diversity within the region (Hilborn *et al.* 2003). Information on the Togiak Chinook salmon population presented here provides baseline data at current conditions with which to track potential long-term changes in spawning distri-

Table 3. Numbers of radio-tagged Chinook salmon ultimately fated to mainstem (main.) or tributary (trib.) spawning locations in the Togiak River by release stratum, 2009–2012

	2009			2010			2011			2012		
Stratum	Dates	Main. fish	Trib. fish	Dates	Main. fish	Trib. fish	Dates	Main. fish	Trib. fish	Dates	Main. fish	Trib. fish
1	25 Jun–4 Jul	12	3	20 Jun–3 Jul	15	8	19 Jun–2 Jul	2	1	21–30 Jun	2	5
2	5–11 Jul	41	5	4–10 Jul	23	11	3–9 Jul	15	2	1–10 Jul	28	9
3	12–18 Jul	25	3	11–17 Jul 17	29	7	10–16 Jul	37	10	11–20 Jul	18	2
4	19 Jul–5 Aug	26	3	18–24 Jul	37	4	17–23 Jul	27	0	21–30 Jul	22	6
5	–	–	–	25 Jul–7 Aug	23	2	23 Jul–6 Aug	18	1	31 Jul–9 Aug	13	0
6	–	–	–	–	–	–	–	–	–	10–12 Aug	1	0

bution and abundance that may result as temperature and hydrological changes associated with global climate manifest (Kovach *et al.* 2012; Leppi *et al.* 2014). Furthermore, the Togiak River is a short river system and provides contrast in watershed size in comparing Chinook salmon life history across the region and across time.

While it is believed that substantial changes to radio-tagged fish behaviour are unlikely in this study, the process of radio tagging may stress fish, potentially leading to changes in movement or spawning behaviour (Bernard *et al.* 1999; Bromaghin *et al.* 2007). Previous radio telemetry studies on adult Chinook salmon movement, however, have shown robustness to gastrically implanted radio-tagging effects (Berman & Quinn 1991; Matter & Sandford 2003; Flannery *et al*. 2012). Several points suggest that radio tagging did not significantly affect the behaviour of adult Chinook salmon in the present study. First, all tagged salmon were large in size relative to the radio tag size. For example, the average radio-tagged fish size from the 2012 field season was 801.8 mm (SD = 74.2 mm). Second, efforts were made to reduce any tagging stress on study fish and to only implant tags into healthy fish. Third, radio-tagged Chinook salmon successfully spawned in all previously known spawning reaches based on aerial surveys of untagged fish. Fourth, observations regarding fish entering Togiak River at the tagging site and at recapture sampling at Gechiak Creek weir indicated that untagged fish, fish tagged with spaghetti tags and radio tags, and fish tagged with only spaghetti tags (2011, 2012 only) showed similar movement timing and dynamics.

In contrast to historical aerial survey information that indicated Chinook salmon spawning activity concentrated in the upper mainstem reaches (Baker *et al.* 2009; Salomone *et al.* 2009), surveys based on radio telemetry during the study period consistently indicated the majority of the Togiak Chinook salmon run spawned in lower

Table 4. Holding behaviour (days) of radio-tagged Chinook salmon in lower mainstem reaches of the Togiak River, 2010–2012

	Year	*n*	Mean	SD	Range
Pooled	2010	140	17.5	7.0	5, 37
	2011	91	15.4	8.5	2, 37
	2012	91	18.2	8.7	3, 40
Mainstem spawners	2010	111	17.5	6.9	5, 37
	2011	77	16.0	8.7	2, 37
	2012	70	19.6	8.9	3, 40
Tributary spawners	2010	29	17.1	7.4	7, 30
	2011	14	12.1	5.8	3, 21
	2012	21	13.2	6.2	4, 25

Table 5. Estimated total run size and harvest rates for Togiak Chinook salmon 2010–2012. Escapement is the estimated in-river abundance minus sport and subsistence harvest that occur in river, and total run includes escapement plus all combined harvest. Estimates are presented as posterior means with 95% credibility intervals in parentheses

	2010	2010 Bias adjusted	2011	2012
Total run	15 379 (10 565, 24 532)	20 959 (10 839, 51 906)	11 240 (7550, 18 116)	18 299 (11 730, 30 772)
Total harvest	6835	6835	5871	6117
Escapement	8544 (3734, 17 693)	14 123 (4003, 45 076)	5369 (1680, 12 246)	12 181 (5616, 24 652)
Total harvest rate	0.47 (0.28, 0.65)	0.38 (0.12, 0.62)	0.55 (0.32, 0.63)	0.36 (0.20, 0.52)
Commercial harvest rate	0.35 (0.21, 0.48)	0.28 (0.09, 0.46)	0.29 (0.17, 0.41)	0.24 (0.14, 0.35)
Sport harvest rate	0.04 (0.02, 0.06)	0.03 (0.01, 0.05)	0.13 (0.08, 0.19)	0.05 (0.03, 0.07)
Subsistence harvest rate	0.08 (0.05, 0.11)	0.06 (0.02, 0.11)	0.13 (0.07, 0.18)	0.06 (0.04, 0.09)

to mid-mainstem habitat. The difference between the spawning distribution estimates may be partially due to effects of the water clarity and channel depth in the lower sections of the mainstem river on visual aerial survey observations. The telemetry surveys and the visual aerial estimates attributed similar spawning habitat use amongst the tributaries, which tended to be shallower and clearer, affording greater accuracy in aerial counts. Within mainstem spawning reaches, lower-river sections were more heavily used by spawning Chinook salmon than upper mainstem reaches, except for 2010, which was a high-water year relative to other years during the study. Anecdotal evidence from Togiak village residents (P. Abraham, personal communication) supports this pattern, observing greater number of Chinook salmon spawning further upriver during high-water seasons. The preponderance of Chinook salmon spawning in larger, mainstem waters of the Togiak River is consistent with Chinook salmon spawning populations preferring mainstem and large tributary habitats in other northern systems (e.g. Yukon River in western Alaska: Bradford *et al.* 2009; Copper River in south central Alaska: Wuttig & Evenson 2001). Although the Togiak River is short (93 rkm), tributary spawning fish appear to have earlier run timing than mainstem spawning fish. This pattern is similar, although not as extreme, to larger Chinook salmon systems in Alaska such as the Kenai or Yukon rivers where early runs are dominated by tributary spawners and late runs by mainstem spawners (Burger *et al.* 1985; Eiler *et al.* 2004).

Information on in-river run timing data for other Bristol Bay Chinook salmon runs for years during the study period is limited, but data available indicate that the Togiak River has later run timing than the Nushagak River. Sonar count data 40 rkm upstream from the mouth of the Nushagak River indicate that Chinook salmon peak run days, measured as maximum daily escapement, for 2009–2012 were Julian days 171, 166, 174 and 177, respectively (Salomone *et al.* 2011; Jones *et al.* 2012, 2013; Buck 2013). By contrast, Togiak River peak run day estimates upstream of the mouth of the river at the study tagging site (see above) in the same years were 193, 196, 197 and 195 (Fig. 2). The Nushagak River is one of the most productive Chinook salmon complexes in the state, with total run sizes above 100 000 (Jones *et al.* 2013). While the Togiak River, which drains a watershed of about 5200 km^2, is considerably smaller than the Nushagak River, which drains a watershed of about 34 700 km^2, the two rivers had similar numbers of salmon returning per km^2 of watershed area over 2010–2012. Mean total run of Chinook salmon per km^2 of watershed for the Togiak River in 2010–2012 was 2.89 using the unadjusted 2010 abundance estimate (3.28 using the bias-adjusted 2010 estimate) compared to mean Chinook salmon per km^2 of watershed for the Nushagak River of 2.81 over the same years (cf. Jones *et al.* 2013).

Mark–recapture sampling in the Togiak River system was generally successful, but as simulation analyses indicated (Data S3), tagging in proportion to abundance is necessary to achieve unbiased estimates when implementing systematic (versus random) recapture sampling. As such, it is cautioned that the population abundance estimates and the associated exploitation rates from 2010 should be viewed with additional uncertainty due to potential bias from induced capture heterogeneity. While attempts were made to adjust estimates for this bias using mark–recapture simulations, the true degree of bias remains undetermined. It is recommended that a field protocol for tag releases for studies using systematic recapture sampling on subcomponents of a salmon run complex should be carefully analysed for potential induced capture heterogeneity. Even with tagging in proportion to abundance, study designs that use systematic recapture samples on tributary weirs are limited to a maximum recapture sample size equal to the tributary run. Precision of Lincoln–Petersen abundance estimates is affected by the tag recapture rate, and thus, these designs will lead to imprecise abundance estimates if tributary runs are small relative to the overall stock complex run size. Studies with similar field designs may wish to consider additional recapture sampling. If tagging effort can be administered such that tag releases are in proportion to run abundance, then a wide range of recapture sampling schemes will result in valid data for the Lincoln–Petersen model. For example, carcass surveys presented low-cost additional recapture sampling to supplement weir projects. Other alternatives can include fish-wheel sampling, hook-and-line sampling or beach seining. The overall time and financial cost of mark–recapture studies relying on weir recapture sampling, particularly in remote locations, are high and may constrain their viability as long-term monitoring solutions for most systems and management budgets. While the option was unavailable during this study, coupling mark–recapture sampling studies with aerial surveys would allow for an aerial survey catchability coefficient, q, to be estimated, which could be used to translate an aerial index, I_a, to an abundance estimate, N: $N = I_a /q$. This could help provide a lower cost option for estimating abundance in future years with only aerial surveys.

Although isolated, the Togiak Chinook salmon run experiences substantial exploitation, with harvest through the terminal drift gillnet fishery and in-river sport and subsistence fisheries estimated at 36–55% over the study period. Furthermore, catch-and-release handling may result in latent mortality, increasing the actual mortality rates associated with sport fishery harvests (Bendock & Alexandersdottir 1993). Estimates of stock–recruitment relationships for western and south-western Alaskan Chinook salmon stocks are rare due to challenges in collecting run size estimate and harvest information necessary to fit stock–recruit curves to determine escapement goals that lead to maximum sustainable yield (Hilborn & Walters 1997; Fleischman *et al.* 2013). Stock recruitment analyses and thus escapement reference points to achieve maximum sustainable yield are not currently available given the short time series of run abundances available for Togiak Chinook salmon; however, observed harvest rates from other western and south-western Alaskan rivers, including the Kuskokwim, Nushagak and Yukon, have been estimated to range in the same order or lower than harvest estimates for the Togiak (Hamazaki *et al.* 2012; CSMT 2013).

The Togiak run represents a northern Chinook salmon population from an undisturbed watershed. For example, only two villages with populations combining to <900 residents exist within the Togiak River watershed, and a substantial portion of the watershed is encompassed by the Togiak National Widlife Refuge. Detailed information on Chinook salmon distribution and migration behaviour provides information that may be applicable to other northern Chinook salmon systems and aid understanding and management of Chinook salmon stocks (Moran *et al.* 2013). For example, holding in freshwater reaches near the mouth of the Togiak River was found to be a common behaviour, and backouts into saltwater also occurred, prolonging exposure of in-migrating fish to commercial, sport and subsistence harvest before moving into upper reaches to spawn. There are few studies documenting holding and backout behaviour for adult Chinook salmon in other systems, but holding and backout behaviours as exhibited by Togiak Chinook salmon would mitigate the effectiveness of temporal closures designed to allow pulses of 'clean' escapement through sport and commercial fisheries, as Chinook salmon remain on the fishing grounds for prolonged periods of time. Furthermore, these behaviours may have implications for effort-controlled harvest management if lower-river holding allows for consistent catch success across low- and high-run years, i.e. presenting a schooling effect that can mask the relationship between catch-per-unit-effort and run size (Arreguin-Sanchez 1996; Pereira & Hansen 2003).

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References

Arreguin-Sanchez F. (1996) Catchability: a key parameter for fish stock assessment. *Reviews in Fish Biology and Fisheries* **6**, 221–242.

Baker T.T., Fair L.F., West F.W., Buck G.B., Fleishman S. & Erikson J. (2009) *Review of Salmon Escapement Goals in Bristol Bay, Alaska, 2006*. Alaska Department of Fish and Game, Fishery Manuscript Series No. 09–05, 66 pp.

Bendock T. & Alexandersdottir M. (1993) Hooking mortality of Chinook salmon released in the Kenai river, Alaska. *North American Journal of Fisheries Management* **13**, 540–549.

Berman C.H. & Quinn T.P. (1991) Behavioural thermoregulation and homing by spring Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *Journal of Fish Biology* **39**, 301–312.

Bernard D.R., Hasbrouck J.J. & Fleischman S. (1999) Handling-induced delay and downstream movement of adult Chinook salmon in rivers. *Fisheries Research* **44**, 37–46.

Blank R.M. (2012) *Letter of Determination of Fishery Resource Disaster to Alaska Governor Sean R. Parnell*. September 12, 2012. Washington, DC: United States Secretary of Commerce, 2 pp.

Bradford M.J., von Finster A. & Milligan P.A. (2009) Freshwater life history, habitat, and the production of Chinook salmon from the Upper Yukon Basin. In: C.C. Krueger & C.E. Zimmerman (eds) *Pacific Salmon: Ecology and Management of Western Alaska's Populations*. Bethesda, MD: American Fisheries Society, pp. 19–38.

Bromaghin J.F., Underwood T.J. & Hander R.F. (2007) Residual effects from fish wheel capture and handling of Yukon River fall chum salmon. *North American Journal of Fisheries Management* **27**, 860–872.

Brookover T.E., Browning J.B., Regnart J.R., Russell R.B. & Weiland K.A. (1996) *Salmon Spawning Ground Surveys in the Bristol Bay Area, Alaska, 1995*. Alaska Department of Fish and Game, Regional Information Report No. 2A96-31, 92 pp.

Buck G.B. (2013) *Sonar Enumeration of Pacific Salmon Escapement into the Nushagak River, 2009*. Alaska

Department of Fish and Game, Fishery Data Series No.13-34, 86 pp.

Bue B.G., Fried S.M., Sharr S., Sharp D.G., Wilcock J.A. & Geiger H.J. (1998) Estimating salmon escapement using area-under-the-curve, aerial observer efficiency, and stream-life estimates: the Prince William Sound pink salmon example. *North Pacific Anadromous Fish Commission Bulletin* **1**, 240–250.

Burger C.V., Wilmot R.L. & Wangaard D.B. (1985) Comparison of spawning areas and times for two runs of Chinook salmon *Oncorhynchus tshawytscha* in the Kenai River, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 693–700.

Clark R.A. (2009) *An Evaluation of Estimates of Sport Fish Harvest from the Alaska Statewide Harvest Survey, 1996–2006*. Alaska Department of Fish and Game, Special Publication No. 09-12, 89 pp.

CSMT (Chinook Salmon Management Team of the Alaska Department of Fish and Game) (2013) *Chinook Salmon Stock Assessment and Research Plan, 2013*. Alaska Department of Fish and Game, Special Publication No. 13-01, 62 pp.

Dye J.E. & Schawnke C.J. (2012) *Report to the Alaska Board of Fisheries for the Recreational Fisheries of Bristol Bay, 2010–2012*. Alaska Department of Fish and Game, Special Publication No. 12–17, 62 pp.

Eiler J.H., Spencer T.R., Pella J.J., Masuda M.M. & Holder R.R. (2004) *Distribution and Movement Patterns of Chinook Salmon Returning to the Yukon River Basin in 2000–2002*. NOAA Technical Memorandum, NMFS-AFSC-148, 110 pp.

Fair L.F., Brazil C.E., Zhang X., Clark R.A. & Erickson J.W. (2012) *Review of Salmon Escapement Goals in Bristol Bay, Alaska*. Alaska Department of Fish and Game, Fishery Manuscript Series No. 12-04, 98 pp.

Flannery B.G., Crane P.A., Eiler J.H., Beacham T.D., Decovich N.A., Templin W.D., *et al.* (2014) Comparison of radiotelemetry and microsatellites for determining the origin of Yukon river Chinook salmon. *North American Journal of Fisheries Management* **32**, 720–730.

Fleischman S.J., Catalano M.J., Clark R.A. & Bernard D.R. (2013) An age-structured state space stock–recruit model for Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 401–414.

Hamazaki T., Evenson M. & Schaberg K.L. (2012). *Spawner-Recruit Analysis and Escapement Goal Recommendation for Chinook salmon in the Kuskokwim River Drainage*. Alaska Department of Fish and Game, Fisheries Manuscript Series No. 12-08, 68 pp.

Hilborn R. & Walters C.J. (1997) *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty*. New York: Chapman & Hall, p 570.

Hilborn R., Quinn T.P., Schindler D.E. & Rogers D.E. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 6564–6568.

Jones M., Sands T., Morstad S., Baker T., Buck G., West F. *et al.* (2012) *2011 Bristol Bay Area Annual Management Report*. Alaska Department of Fish and Game, Fishery Management Report No. 12–21, 136 pp.

Jones M., Sands T., Morstad S., Salomone P., Buck G., West F. *et al.* (2013) *2012 Bristol Bay Area Annual Management Report*. Alaska Department of Fish and Game, Fishery Management Report No. 13-20, 132 pp.

Kovach R.P., Gharrett A.J. & Tallmon D.A. (2012) Genetic change for earlier migration timing in a pink salmon population. *Proceedings of the Royal Society B* **279**, 3870–3878.

Krebs C. (1999) *Ecological Methodology*, 2nd edn. New York: Addison Wesley, p. 624.

Leppi J.C., Rinella D.J., Wilson R.R. & Loya W.M. (2014) Linking climate change projections for an Alaskan watershed to future coho salmon production. *Global Change Biology* **20**, 1808–1820.

Lunn D.J., Thomas A., Best N. & Spiegelhalter D. (2000) WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* **10**, 325–337.

Matter A.L. & Sandford B.P. (2003) A comparison of migration rates of radio- and PIT-tagged adult Snake river Chinook salmon through the Columbia river hydropower system. *North American Journal of Fisheries Management* **23**, 967–973.

Moran P., Teel D.J., Banks M.A., Beacham T.D., Bellinger M.R., Blankenship, S.M. *et al.* (2013) Divergent life-history races do not represent Chinook salmon coast-wide: the importance of scale in Quaternary biogeography. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 415–435.

Pereira D.L. & Hansen M.J. (2003) A perspective on challenges to recreational fisheries management: summary of the symposium on active management of recreational fisheries. *North American Journal of Fisheries Management* **23**, 1276–1282.

Pollock K.H., Nichols J.D., Brownie C. & Hines J.E. (1990) Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**, 3–97.

R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at www.R-project.org.

Salomone P., Morstad S., Sands T. & Jones M. (2009) *Salmon Spawning Ground Surveys in the Bristol Bay Area, Alaska, 2008*. Alaska Department of Fish and Game, Fishery Management Report No. 09-42, 63 pp.

Salomone P., Morstad S., Sands T., Jones M., Baker T., Buck G. *et al.* (2011) *2010 Bristol Bay Area Annual Management Report*. Alaska Department of Fish and Game, Fishery Management Report No. 12–23, 148 pp.

Sands T. (2012) *Overview of the Bristol Bay Salmon Fishery 2010–2012, a Report to the Alaska Board of Fisheries*. Alaska Department of Fish and Game, Special Publication No. 12-18, 16 pp.

Schindler D., Krueger C., Bisson P., Bradford M., Clark B., Conitz, J. *et al.* (2013) *Arctic-Yukon-Kuskokwim Chinook salmon Research Action Plan: Evidence of Decline of Chinook Salmon Populations and Recommendations for Future*

Research. Artic-Yukon-Kuskokwim Sustainable Salmon Initiative Research Action Plan, 70 pp.

Seber G.F. (2002) *The Estimation of Animal Abundance and Related Parameters*, 2nd edn. Caldwell: Blackburn Press, p 654.

Sturtz S., Ligges U. & Gelman A. (2005) R2WinBUGS: A package for running WinBUGS from R. *Journal of Statistical Software* **12**, 1–16.

USFWS (U.S. Fish and Wildlife Service) (1990) *Fishery Management Plan, Togiak National Wildlife Refuge*. Dillingham, AK: U.S. Fish and Wildlife Service, King Salmon Fishery Resource Office and Togiak National Wildlife Refuge, 80 pp.

Winter J.D. (1983) Underwater biotelemetry. In: L.A. Nielsen & D.L. Johnson (eds) *Fisheries Techniques*. Bethesda, MD: American Fisheries Society, pp. 371–395.

Wuttig K.G. & Evenson M.J. (2001) *Inriver Abundance, Spawning Distribution, and Migratory Timing of Copper River Chinook salmon in 2000*. Alaska Department of Fish and Game, Fishery Data Series No. 01–22, 61 pp.

Zar J.H. (2010) *Biostatistical Analysis*, 5th edn. Upper Saddle River, NJ: Pearson, p 960.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Schedule of tagging, tracking, and recapture efforts for Chinook salmon sampling in Togiak River 2009–2012.

Table S2. Number of Togiak Chinook salmon harvested in 2010–2012.

Data S1. Run timing estimation model.

Data S2. Bayesian implementation of the Lincoln-Petersen estimator.

Data S3. Simulation model for abundance bias due to induced capture heterogeneity from scheduled tag releases.

Data S4. Supplementary materials reference list.