Monitoring of grizzly bear population trends and demography using DNA mark–recapture methods in the Owikeno Lake area of British Columbia

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Abstract: We used DNA sampling and mark–recapture modeling to estimate population trend(s), population size, and the demographic response of a coastal British Columbia grizzly bear population (*Ursus arctos* L., 1758) to low salmon escapement levels from 1998 to 2002. We contrasted the demography of three sampling areas in response to temporal and spatial variation in salmon availability. Population trend (λ) estimates suggested that salmon availability was too low in the first 2 years of the study to sustain grizzly bear populations. One of the sampling areas exhibited higher levels of salmon availability in later years of the study, leading to increased rates of addition. Apparent survival rates increased in all areas potentially as a result of increased salmon availability. Joint interpretation of λ and superpopulation estimates allowed for the assessment of whether salmon availability levels were high enough to sustain current population sizes of grizzly bears on salmon streams. This study illustrates how joint modeling of separate sampling areas can be used to assess spatial variation in population demography and population trends, as well as increase precision of estimates for individual sampling areas. It also illustrates how DNA mark–recapture can be used as a methodology to explore the effects of changes in environmental conditions on population demography and population trend of grizzly bears or of other wildlife species.

Résumé : L'échantillonnage de l'ADN et une modélisation de marquage–recapture nous ont servi à estimer la tendance démographique, la taille de la population et la réaction d'une population côtière de grizzlis (*Ursus arctos* L., 1758) de la Colombie-Britannique à des niveaux faibles d'échappement de saumons de 1998 à 2002. Nous avons comparé dans trois sites d'échantillonnage la démographie des grizzlis en réaction à des variations temporelles et spatiales de la disponibilité des saumons. Les estimations de la tendance (λ) indiquent que la disponibilité des saumons était trop basse durant les deux premières années de l'étude pour le maintien des populations de grizzlis. Dans un des sites d'échantillonnage, la disponibilité plus élevée des saumons dans les dernières années de l'étude a entraîné des taux d'addition accrus. Les taux de survie apparente ont augmenté dans tous les sites, probablement à cause de la disponibilité accrue des saumons. L'interprétation conjointe des estimations de λ et de la superpopulation nous a permis d'évaluer si la disponibilité des saumons est assez élevée pour supporter les densités actuelles des populations de grizzlis près des cours d'eau à saumons. Notre étude illustre comment la modélisation simultanée de plusieurs sites différents d'échantillonnage peut servir à évaluer la variation spatiale de la démographie et des tendances de la population et à augmenter la précision des estimations dans les différents sites individuels d'échantillonnage. Elle montre aussi comment la méthode de marquage–recapture avec l'ADN peut servir à explorer les effets des changements des conditions environnementales sur la démographie et les tendances de la population chez les grizzlis ou d'autres espèces de gibier sauvage.

[Traduit par la Rédaction]

Introduction

One of the most challenging issues in grizzly bear (*Ursus arctos* L., 1758) conservation has been the estimation of population abundance and population trend. Recently, DNA mark–recapture methods have been used to estimate population size based on intensive sampling of small study areas within a single year (Woods et al. 1999; Mowat and Strobeck 2000; Poole et al. 2001; Boulanger et al. 2002). Although these studies have provided unprecedented estimates

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of population size, they have not provided estimates of population trend. Estimates of population trend are an essential piece of information required for the evaluation of the population response to changes in management practices and environmental conditions.

We became interested in the application of DNA methods to estimate grizzly bear population trend given the recent advances in genetic marking and mark–recapture modeling. Recent mark–recapture literature (Pradel 1996; Hines and Nichols 2002; Nichols and Hines 2002; Sandercock and Beissinger 2002) suggests that mark–recapture models which estimate apparent survival and population trend are robust to heterogeneity of capture probabilities and violation of population closure, two issues that challenge the estimation of population size (Boulanger and McLellan 2001; Boulanger et al. 2002). In addition, new models such as the Pradel (1996) model allow for the exploration of population demography and environmental factors that influence demography through the use of covariates (Franklin 2001).

Of particular conservation interest was the status and population trend of grizzly bears in the Owikeno Lake area of British Columbia. This area has seen historical declines in salmon escapement (Fig. 1) that have potentially affected grizzly bear populations owing to the coastal grizzly bears' reliance on salmon as a principal food source (Welch et al. 1997; Hilderbrand et al. 1999). In addition to estimation of population trend, we were interested in the grizzly bear population demographic response to low salmon escapement. If grizzly bear populations are reliant on salmon, then it would be expected that population abundance and demography of grizzly bears would be associated with salmon availability levels. At the onset of the study, salmon escapement was lower than historic levels, and during the study, escapement declined to historically low levels followed by minor recoveries in many of the rivers (Fig. 1).

The only statistical estimates of population trend for grizzly bears have come from long-term studies of radio-collared bears (Eberhardt et al. 1994; Hovey and McLellan 1996) and helicopter count indices. Radio-collar studies have used estimates of survival and reproductive rate to estimate population rate of change (λ) using the Leslie matrix and related population viability analysis (PVA) methods (Boyce et al. 2001). This approach was not optimal for the Owikeno area owing to the remoteness of the study area and the short sampling time (i.e., a few months of the year), both factors making it difficult to maintain a suitable number of radio-collared bears. In addition, we suspected that the populations of grizzly bears were under stress as a result of declining salmon stocks; therefore, many of the assumptions required to estimate λ using PVA methods, such as time-invariant population parameters and a stable age distribution of grizzly bears, would be violated. Sandercock and Beissiger (2002) compared the Pradel model, PVA methods, and count indices as methods to estimate population trend for green-rumped parrolets, *Forpus passerinus* (L., 1758), and found that the Pradel model displayed the best performance when compared with count indices and PVA methods. Sandercock and Beissinger (2002) concluded that the Pradel model was optimal for populations where less information was available, a scenario that applied to the Owikeno grizzly bear population.

Fig. 1. Trends in historic sockeye salmon, *Oncorhynchus nerka*, escapement for tributaries of Owikeno Lake from Fisheries and Oceans Canada surveys (Rutherford et al. 1998; Department of Fisheries and Oceans 2002). Each line represents a tributary river. Data were smoothed with a spline function using a tension value of 35. This study was conducted from 1998 to 2002.
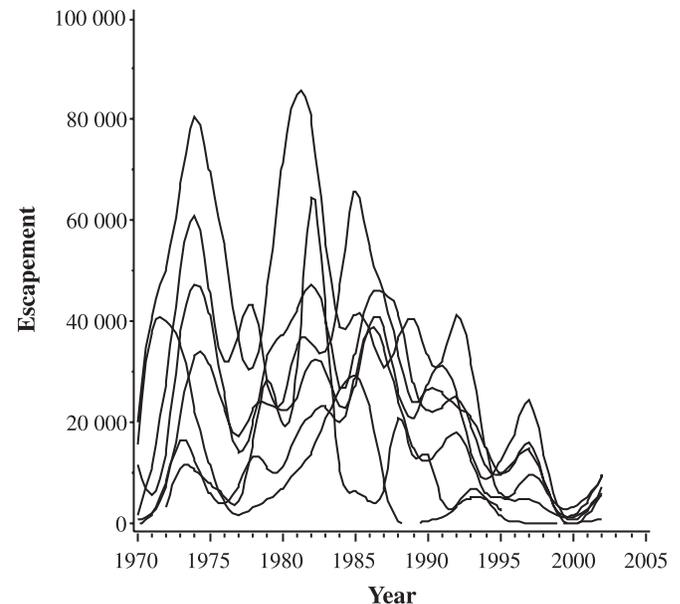
In this paper we use the Pradel model to explore the relationship between grizzly bear population trend, demography, and varying levels of salmon availability from 1998 to 2002. Our emphasis is the use of DNA mark–recapture to contrast the demography and population trends of grizzly bears from three sampling areas that have experienced different levels of salmon abundance. In addition, we also explore the use of methods to estimate population size as a means to complement the estimation of population trend. We compare this approach to more traditional estimates of population trend based on helicopter count indices. Although this case study focuses on grizzly bears, the general analysis methodologies should be applicable to other species.

Materials and methods

Study area

The study area was located approximately 60 km south of Bella Coola on the coast of British Columbia. The core of the study area encompassed all of the streams flowing into Owikeno Lake, and the Chuckwalla and Kilbella rivers flowing into Rivers Inlet (Fig. 2). Topography is rugged, with elevations from sea level to over 1900 m. Major terrain units include estuaries, level fluvial areas (floodplain), some upslope units with very shallow soils over bedrock, numerous avalanche tracks, colluvial and alluvial fans, alpine tundra, ice fields, sedge fens, and organic bogs. There is no direct road access to this area; all access is through float plane or boat. Logging roads are present in this area, but these roads terminate at ocean or lake inlets with all logging equipment being barged into the area.

Dominant tree species included western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), amabilis fir (*Abies amabilis*

Fig. 2. Owikeno Lake study area showing Owikeno Lake, which is located 60 km south of Bella Coola on the coast of British Columbia. Each symbol represents a DNA monitoring site. The Chuckwalla–Ambach (middle left), Washwash–Inziana (upper right), and Neechanz–Genesee (lower right) sampling areas are shown.
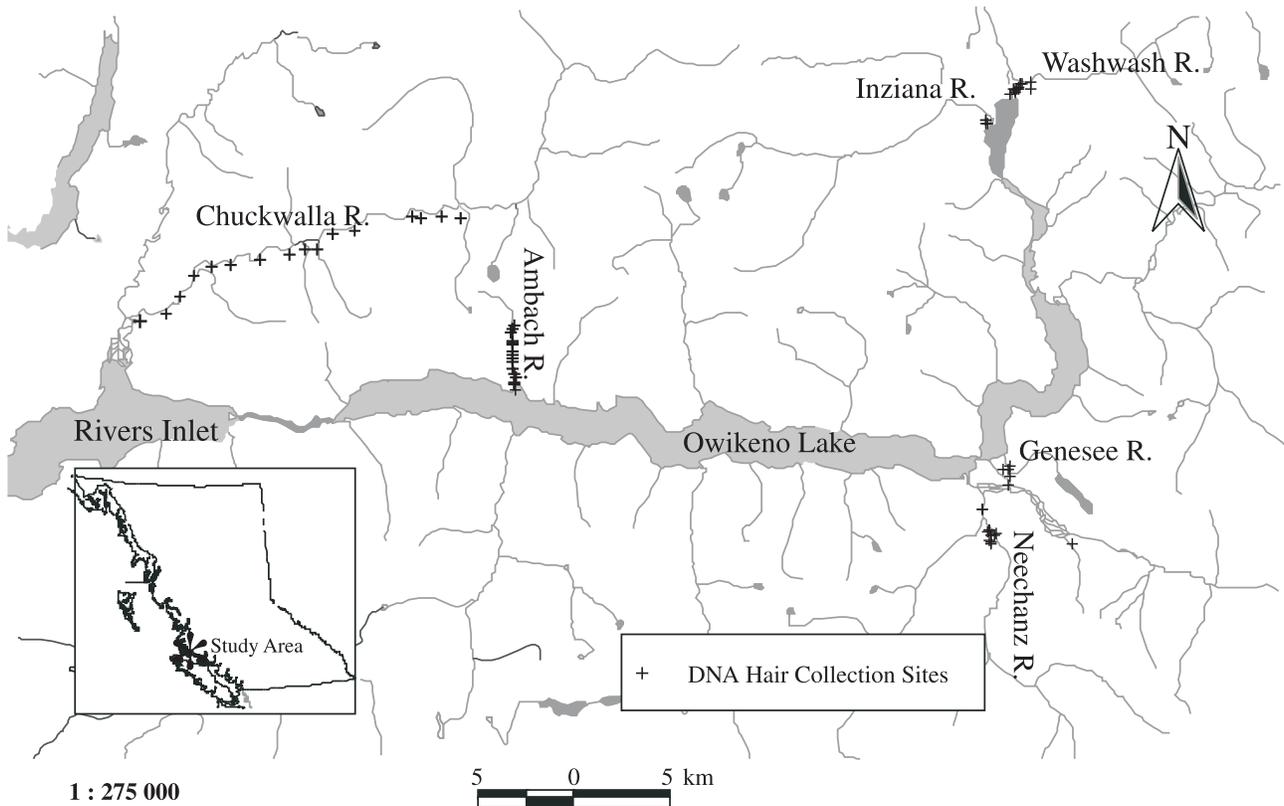
(Dougl. ex Loud.) Dougl. ex Forbes), and western red cedar (*Thuja plicata* Donn ex D. Don). Sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) is the dominant salmon species in the rivers flowing into Owikeno Lake. Four other species of Pacific salmon are also found in the rivers and streams of the study area, including chinook salmon (*Oncorhynchus tshawytscha* Walbaum in Artedi, 1792), coho salmon (*Oncorhynchus kisutch* (Walbaum, 1792)), chum salmon (*Oncorhynchus keta* (Walbaum in Artedi, 1792)), pink salmon (*Oncorhynchus gorbuscha* (Walbaum, 1792)), as well as steelhead (*Oncorhynchus mykiss* (Walbaum, 1792)), rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), cutthroat trout (*Oncorhynchus clarkii* (Richardson, 1836)), and Dolly Varden char (*Salvelinus malma* (Walbaum in Artedi, 1792)).

Field methods

DNA sampling was conducted using barbed wire sampling (Woods et al. 1999) in the three core sampling areas of salmon-feeding by grizzly bears in the Owikeno study (Fig. 2). Sampling was conducted during peak sockeye salmon runs during the fall (September and October). The density of sites was different for areas owing to the size of the three areas where grizzly bears congregated to feed on salmon, and the topography and logistics of accessing sites. The Neechanz–Genessee sampling area had a total of 23 wire sites (7.6 km of river sampled); the Inziana–Washwash sampling area had a total of 26 wire sites (3.5 km of river sampled); and the Chuckwalla–Ambach sampling area had

12 wire sites (27 km of river sampled). The Chuckwalla–Ambach sites were in different drainages connected by a low pass; therefore, they could be considered one connected sampling area. All sites were accessed by river using jet boat, river raft, helicopter, or logging road. Unlike spring-based DNA sampling (sensu Woods et al. 1999), no bait was used to attract grizzly bears to the sites. Double-strand barbed wire was tightly stretched and stapled between two trees across grizzly bear trails so that when the grizzly bears traveled along the trail they were likely to pass under the wire. The barbed wire was strung approximately 50 cm off the ground (slightly higher than the shoulder height of a 2.5-year-old grizzly bear). Criteria influencing site selection was evidence of recent grizzly bear activity, presence of spawning salmon, and presence of grizzly bear marked trees and grizzly bear trails. Areas with topographical constrictions that funnel travel through a smaller area were also chosen. At some sites, other wire techniques were used in an attempt to maximize hair collection. For example, wire was strung diagonally from tree trunks to sturdy roots or strung under large logs across stream channels. Whenever possible, sites were alternated from one side of the river to the other. Sites were checked every 3–8 days because of differences in the proximity to the field camp. The number and distribution of sites were kept constant for each area throughout the study; however, the number of sampling sessions was varied for different years of the study because of logistical and funding constraints. Timing of yearly sampling was coordinated with peak salmon abundance as determined by on-site

Table 1. Principal candidate models for mark–recapture analysis of the Owikeno Grizzly Bear DNA Mark–Recapture Project, 1998–2002.

Hypothesis about bear demography	Model(s)
Is influenced by river-specific salmon availability	ϕ(area × salmon) or f(area × salmon); ϕ(area + salmon) or f(area + salmon)
Is influenced by overall salmon availability with similar relationships between rivers	ϕ(salmon) or f(salmon)
Is synchronized between areas but not influenced by availability	ϕ(time) or f(time); ϕ(linear trend) or f(linear trend)

Fisheries and Oceans Canada personnel. Data from multiple sessions were pooled into one yearly session for mark–recapture analysis. Genetic analysis of DNA samples was conducted using the techniques described in Woods et al. (1999) and Paetkau (2003).

Salmon availability indices that considered both the level of escapement and the availability of fish in the area were used to allow field comparisons of temporal trends in annual river survey, as well as comparisons of rivers within the Owikeno system. Escapement was not necessarily proportional to availability. For example, escapement may be high, but if water levels were also high, then it may be difficult for grizzly bears to capture salmon, thus creating low availability. Salmon availability was rated by adapting a standardized methodology developed for habitat suitability ratings in British Columbia (Resources Inventory Committee 1999). Each river was compared with the benchmark Atnarko River, and the relative difference in annual escapement (Department of Fisheries and Oceans 2002) was expressed as a percent category (0%, 1%–5%, 6%–25%, 26%–50%, 51%–75%, 76%–100%). The category was then adjusted for availability by considering the length of river with spawning salmon, bank and gravel bar characteristics, number of spawning reaches, and water levels during the time of DNA sampling. The benchmark Atnarko River, located 65 km from Owikeno Lake, has annual salmon escapement of greater than 1 million from five salmon species in most years and escapements have been stable for the past 20 years. The index was estimated by the same individual (S. Himmer) each year to ensure consistency. For analyses, the midpoint percentage of each category was used to compare different rivers, as well as population trends in individual rivers, over time.

Helicopter surveys were flown just before sunrise to produce estimates of population trend and count indices for each river course that could be compared with DNA estimates. The Chuckwalla, Ambach, Inziana, Washwash, Neechanz, and 12 other rivers in the vicinity of Owikeno Lake were surveyed in two blocks based on geographic proximity. The rivers were flown at 50–70 knots (1 knot = 1.852 km/h) ground speed at or slightly above tree top level. Each river was flown at the same time each survey period using the same sighting techniques, flight speed, and helicopter altitude. Between 3 and 8 replicate surveys were conducted on each river during the same time as DNA surveys for each year of the project. Population trend (λ) was estimated by the geometric mean of the ratio of mean yearly counts (i.e., $\lambda_{t+1} = C_{t+1}/C_t$ where C_{t+1} and C_t were counts from successive years) from each of the survey blocks.

Mark–recapture analysis

The Pradel open mark–recapture model (Pradel 1996) was used to analyze the mark–recapture data as implemented in the program MARK (White and Burnham 1999). The form of Pradel's model used for this analysis estimates apparent survival, recapture rate, rate of additions, and population rate of change as a derived parameter. Apparent survival (ϕ) is the probability that a grizzly bear stays in the population between two sampling intervals. Apparent survival includes both mortality and emigration, since in both cases the grizzly bear would no longer be available for capture in subsequent sessions. Recapture rate (p) is the rate of recapture of marked grizzly bears in the population. Rate of addition (f) is the number of new individuals in the populations at time $j + 1$ per individual at time j that includes both immigration and births between two sampling years. Apparent survival and rate of addition can be added to obtain an estimate of λ, the population rate of change ($\lambda_j = \phi_j + f_j$). The population rate of change (λ) also relates to population size by $N_{t+1} = \lambda N_t$ where N is the population size at times t and $t + 1$ (Franklin 2001).

Each of the three sampling areas was entered as a group in the mark–recapture analysis to allow separate estimates of model parameters and to test a priori hypothesis about the comparative demography of each sampling area. One issue that complicated comparison of areas was the different degree of sampling effort and trap density in each area that may have created differences between recapture rates of grizzly bears. For this reason, recapture rate was modeled as a function of site days that sites were available to grizzly bears for each season and sampling area.

One of the main research questions was whether the demography of grizzly bears was influenced by the comparative availability of salmon in each of the sampling areas. Following Burnham and Anderson (1998), a priori hypotheses were constructed about the potential relationship between the rate of additions (f), or apparent survival rate (ϕ), and salmon availability (Table 1). It was hypothesized that grizzly bears might immigrate to streams with increased salmon availability levels or emigrate from areas with lessened salmon availability. This relationship was potentially different for each river or similar for all rivers. Of critical interest was whether there was a threshold level of salmon availability that was needed to maintain populations of grizzly bears at feeding areas. It was hypothesized that the relationship between salmon availability and apparent survival or rates of addition could be linear or asymptotic (approximately quadratic), as there may be a level of salmon in which the population of grizzly bears becomes saturated with fish. In addition, combinations of hypotheses were considered. For example, it was plausible that larger scale factors influenced demography in addition to river-specific salmon availability. In this case, it would be expected that a

Table 2. Summary of mark–recapture effort and data for the Owikeno Grizzly Bear DNA Mark–Recapture Project, 1998–2002.

Sampling area and year	Effort (site days)	Salmon availability[a]	Number of grizzly bears captured	Number of grizzly bears recaptured during			
				1999	2000	2001	2002
Neechanz–Genesee							
1998	786	38.0	28	4	2	4	0
1999	207	14.4	4		1	1	
2000	183	38.0	3			2	
2001	289	59.4	12				
2002	579	63.0	20				
Chuckwalla–Ambach							
1998	660	32.2	19	2	0	4	0
1999	148	52.5	3		1	1	0
2000	614	63.0	3			1	1
2001	632	83.8	26				12
2002	672	88.0	23				
Washwash–Inziana							
1998	722	38.0	16	0	0	0	3
1999	119	3.0	3		0	0	0
2000	185	38.0	0			0	0
2001	199	38.0	2				0
2002	366	63.0	10				

[a]Adjusted percent difference of salmon availability from the benchmark river.

model that considered similar time-specific rates in addition to availability of salmon (ϕ(time + availability)) would be supported by the data.

Relative model fit was assessed using sample-size-adjusted Akaike Information Criterion (AIC_c) model selection method (Burnham and Anderson 1998). Models with the lowest AIC_c scores were considered most supported by the data. Delta AIC_c values were also used to evaluate the fit of models when their AIC_c scores were close. In general, any model with a ΔAIC_c score of less than 2 was most supported by the data. Estimates were model-averaged to account for uncertainty in model selection. Goodness of fit was tested and overdispersion parameters were estimated using the Cormack–Jolly–Seber model with program RELEASE (Burnham et al. 1987) under the assumption that overdispersion could be estimated from the recapture portion of the encounter history. If overdispersion was detected, then quasi-AIC_c ($QAIC_c$) methods were used for model selection instead of AIC_c methods (Burnham and Anderson 1998). A logit link was used for all analyses.

The cumulative population of grizzly bears using salmon streams in a given year (termed "superpopulation" in White 1996) was estimated using an estimator derived by McDonald and Amstrup (2001). This estimator basically uses the number of unique grizzly bears captured annually divided by the estimated recapture rate from the Pradel model to estimate population size. Model-averaged estimates of recapture rate were used to estimate population size, thus allowing for the consideration of multiple models.

Results

One hundred and twenty-three grizzly bears were identified over the course of 5 years of monitoring at the three sampling areas. The number of grizzly bears recaptured is summarized in the recaptured grizzly bears columns in Table 2. For example, 28 grizzly bears were captured in 1998 on the Neechanz–Genesee sampling area in which 4, 2, 4, and 0 were recaptured in 1999, 2000, 2001, and 2002, respectively. It can be seen that there were no recaptures on the Washwash–Inziana sampling area, except for three bears recaptured in 2002 that were initially captured in 1998. Observation of effort shows that except for the Chuckwalla–Ambach sampling area the effort was reduced in 1999, 2000, and 2001 compared with the effort in 1998. Salmon availability was lowest in 1999 but then increased for all rivers, with the greatest availability of salmon occurring in the Chuckwalla–Ambach sampling area. Of the 123 grizzly bears identified, only 4 (3 male, 1 female) moved between sampling areas over the course of 5 years of monitoring.

Overdispersion was not detected by the program RELEASE goodness-of-fit tests (χ^2 = 2.9, df = 7, P = 0.89), so AIC_c methods were used for model selection. A model that had river-specific capture probability and effort curves was used to account for differences in capture probabilities between rivers and differences in effort between years. This model was most supported by the data compared with time-specific or constant capture probability models (Table 3 and Fig. 3). Capture probability curves suggested high capture probabilities for the Neechanz–Genesee sampling area where site density was highest, and reduced capture probabilities for the Washwash–Inziana and Chuckwalla–Ambach sampling areas where site densities were lower.

AIC_c model selection results suggested that rates of addition (f) were influenced by salmon availability and other nondefined temporal trends that were similar for all sampling areas (Table 3, model 1). Apparent survival (ϕ) was different for sampling areas and increased linearly throughout

Table 3. Model selection results of Akaike's information criterion adjusted for small sample sizes (AIC$_c$) for the Owikeno Grizzly Bear DNA Mark–Recapture Project, 1998–2002.

No	Apparent survival	Rate of addition	AIC$_c$	ΔAIC$_c$	w_i	K	Deviance
1	Area + linear trend	Time + salmon, salmon^2	505.3	0.00	0.433	16	309.8
2	Area + salmon	Time + salmon, salmon^2	506.8	1.55	0.200	16	311.4
3	Area	Time + salmon, salmon^2	507.6	2.34	0.134	15	314.6
4	Area	Area	509.2	3.90	0.062	11	325.6
5	Linear trend	Time	509.5	4.24	0.052	12	323.6
6	Area + linear trend	Time	510.4	5.15	0.033	14	319.8
7	Linear trend	Time + salmon	510.7	5.43	0.029	13	322.4
8	Area + linear trend	Time + salmon	510.9	5.66	0.026	15	317.9
9	Constant	Time	511.6	6.32	0.018	11	328.0
10	Time	Time	513.8	8.54	0.006	14	323.2
11	Constant	Time + salmon, salmon^2	514.6	9.32	0.004	13	326.3
12	Salmon	Time + salmon, salmon^2	515.9	10.61	0.002	13	327.6
13	Constant	Area × salmon	518.7	13.44	0.001	13	330.5
14	Area + linear trend	Area + salmon	519.4	14.07	0.000	14	328.7
15	Area + linear trend	Area × salmon	520.9	15.64	0.000	16	325.4
16	Area	Area × salmon	522.1	16.81	0.000	15	329.1
17	Area × time	Area × time	554.8	49.47	0.000	39	293.1
18	Constant	Constant	630.8	125.54	0.000	3	464.7

Note: ΔAIC$_c$, the difference in AIC$_c$ values between the *i*th model and the model with the lowest AIC$_c$ value; w_i, Akaike's weights; and K, number of parameters. River-specific recapture rates were modeled (i.e., p(river × effort)) for all models except model 18 where the recapture rate was constant.

Fig. 3. Relationship between recapture probability and site days of effort for each study area. Model-averaged recapture probability are shown for the Neechanz–Genesee (□), Chuckwalla–Inziana (◆), and Washwash–Inziana (△) sampling areas. Error bars represent unconditional SEs. Models from Table 3 were used for model-averaging.
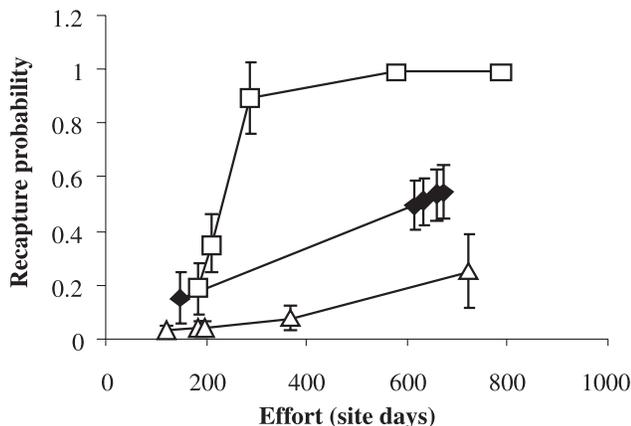
the study (model 1). However, the relationship between salmon availability and apparent survival was weaker but still noteworthy given the lower support of model 2 than for model 1. Models that considered river-specific relationships between salmon availability and rates of addition and apparent survival were less supported by the data.

Inspections of model-averaged estimates of apparent survival, rates of addition, and population rate of change suggest an increase in all parameters over the course of the study (Fig. 4). Apparent survival was lowest for the Neechanz–Genesee and Chuckwalla–Ambach sampling areas in 1999 but slowly increased to higher levels in later years of the study. Rate of addition was close to 0 in 1999

and 2000, followed by a burst of new grizzly bears in the Chuckwalla–Ambach sampling area in 2001, followed by moderate additions in all rivers in 2002. Rate of addition for the Chuckwalla River was lower than for the other rivers in 2002; however, this rate is the ratio of new individuals in 2002 per individuals in 2001. Therefore, this rate was lower partially because of the larger number of individuals in 2001. All sampling areas had negative population growth in 1999 and 2000, followed by positive population growth in 2001 and 2002 as estimated by λ values.

Superpopulation estimates (Table 4) also suggested a decline in population size in 1999 and 2000, followed by increases in 2001 and 2002 for the Chuckwalla–Ambach and Neechanz–Genesee sampling areas. Estimates of superpopulation were similar to the number of grizzly bears identified for the Neechanz–Genesee sampling area in 1998 and 2001 owing to high capture probabilities (Fig. 3). Coefficients of variation of estimates were initially high, then declined to acceptable levels (CV < 20%) in 2002, suggesting reasonable precision of estimates. Note that these estimates correspond to the cumulative number of grizzly bears identified throughout sampling rather than a point estimate. Estimates were not possible for the Washwash–Inziana sampling area as a result of the low numbers of captured grizzly bears (Table 2).

Comparison of DNA superpopulation estimates and helicopter count indices suggested similar relative trends in population size for the Chuckwalla–Ambach and Neechanz–Genesee sampling areas (Table 4). One discrepancy was in the Chuckwalla–Ambach sampling area in 2001 where the superpopulation estimate and the Pradel model λ estimate (Fig. 4) suggested an increase in population size, but the helicopter count index suggested a stable population. Estimates of λ from surveys of the Owikeno watershed and surrounding area suggested a decline in population size from 1998 to 2001 (λ = 0.80, SE = 0.211, *n* = 3 years), followed by a pos-

Table 4. Superpopulation estimates from DNA surveys and count indices from helicopter surveys for the Owikeno Grizzly Bear DNA Mark–Recapture Project, 1998–2002.

Sampling areas and year	Superpopulation estimates			Count indices		
	$\hat{N}$	SE of $\hat{N}$	CV* (%)	C	SE of C	n
Neechanz–Genesee						
1998	28	0.5	0.0	6.4	3.4	8
1999	11	4.9	43.3	0.5	0.5	8
2000	16	9.8	60.3	1.4	0.8	7
2001	15	1.4	9.5	3.1	1.2	8
2002	20	0.5	2.2	0.5	0.8	6
Chuckwalla–Ambach						
1998	36	5.8	16.2	11.3	6.7	4
1999	20	12.8	63.9	8.6	3.8	5
2000	6	2.6	42.5	8.7	1.5	3
2001	51	7.2	14.2	5	1.2	4
2002	42	6.2	14.6	9.3	2.9	3

*CV, coefficient of variation.

Fig. 4. Model-averaged estimates of the rate of emigration/deaths (apparent survival), births/immigration (addition), and λ from the re-parameterized Pradel model. The width of the circles is proportion to the availability of salmon for a given year (as listed in Table 2). Estimates from the Chuckwalla–Ambach (broken circles), Neechanz–Genesee (shaded circles), and Washwash–Inziana (solid circles) sampling areas are shown. Error bars represent unconditional SE estimates. Models from Table 3 were used for model-averaging.
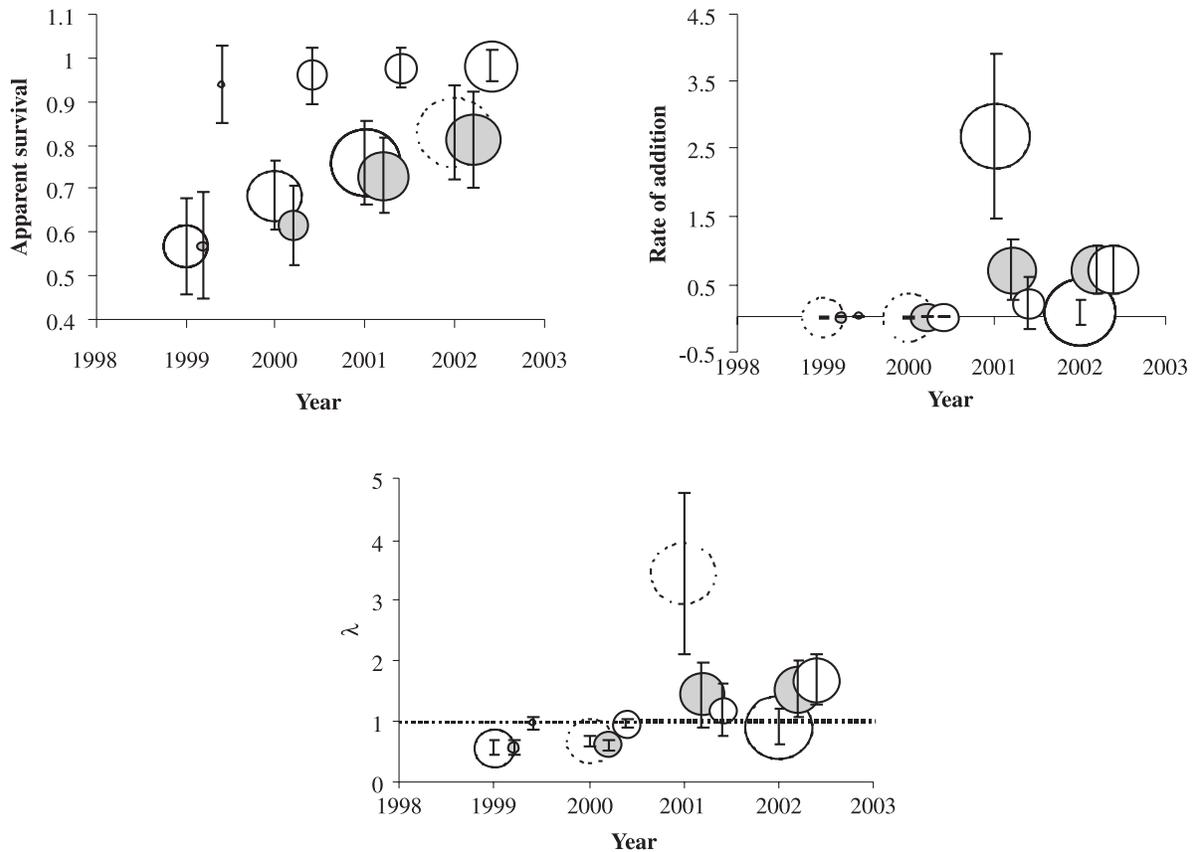
itive trend in population size from 2001 to 2002 (λ = 1.12, SE = 0.25, n = 2 years).

Discussion

The results of this study suggest a dynamic system in which the demography of grizzly bear populations at salmon streams changed dramatically in association with observed levels of salmon availability. Of particular interest was the low apparent survival rates and rates of addition of grizzly bears at all sampling areas in 1999 and 2001, which led to negative population declines as estimated by λ values that

were less than 1 (Fig. 4). The association of these parameters with salmon availability suggests that salmon availability was too low during this time to sustain the populations of grizzly bears in these areas, leading also to declines in superpopulation estimates. In latter years of the study, salmon availability did increase, leading potentially to increased apparent survival and an influx of new grizzly bears presumably from other geographic areas.

This study illustrates how data sets from different sampling areas can be pooled and covariates can be used to enhance estimate precision and contrast the demography of different sampling areas. It would have not been possible to obtain precise estimates for most of the sampling areas without this approach. For example, the Pradel model with time-specific parameter estimates without covariates has 39 parameters (Table 3, model 17), whereas the most supported covariate model with time-specific parameter estimates had 16 parameters (Table 3, model 1) with resulting increases in precision of estimates. In addition, comparison of the demography of the three sampling areas provided further insight into spatial variation in population trends and into factors affecting population trends than would monitoring of one larger area. However, low sample sizes of areas such as the Washwash–Inziana sampling area should still be considered when interpreting estimates. It will take more years of data to allow for the solid evaluation of demography in this sampling area.

One important assumption of this analysis is that the number of grizzly bears identified on salmon streams is indicative of the overall size and status of grizzly bear numbers in the Owikeno area. This assumption could be violated if other foods such as berries are available for grizzly bears to switch to when salmon availability is low. However, published studies of coastal grizzly bears indicate that they are highly reliant on salmon resources. As Hilderbrand et al. (1999) states "We conclude that the availability of meat, particularly salmon, greatly influences habitat quality for brown bears at the individual and population level." Helicopter count surveys also suggested declines in populations from 1998 to 2001 followed by slight increases in 2002, suggesting that the population trends estimated from the DNA study are representative of the overall Owikeno area. Thus, the observed decline in grizzly bears at salmon streams is most likely an indicator of overall population health in the Owikeno Lake area.

The population trends observed in this study are probably not typical of grizzly bear populations in coastal British Columbia given that most fish stocks have not seen such a large decline in escapement as in the Owikeno Lake area. Grizzly bears have been shown to display a large degree of yearly fidelity to salmon streams (MacHutchon et al. 1993; Sellers and Aumiller 1994); therefore, changes in apparent survival probably reflect some degree of mortality rather than just dispersal to other streams. The low number of grizzly bears captured at more than one study area (4) over the course of monitoring also suggests a reasonable level of fidelity to feeding areas. The relatively high rate of additions of grizzly bears to many of the rivers in 2001–2002 (Fig. 4), as indicated by the large number of new grizzly bears in 2001–2002 samples (Table 2), was probably due to new grizzly bears moving into feeding areas vacated by grizzly bears in

earlier years of the study. For example, in late October 1999, subsequent to DNA surveys, 10 grizzly bears were either killed in control actions or relocated from the Owikeno Village that was 10 km from the Chuckwalla–Ambach sampling area. Most of these grizzly bears were probably active in the adjacent Chuckwalla–Ambach area. Removal of these grizzly bears most likely depressed survival rates and eventually allowed other grizzly bears to move into the area as evidenced by the apparent increase in rates of addition in 2001 (Fig. 4).

Importance of interpreting λ and N simultaneously

The grizzly bear population in this study is most likely below historic levels because of decreasing salmon escapement prior to the onset of the study (Fig. 1). Thus, interpretation of the relationship between population trend and demography and salmon availability levels (Fig. 4) should be done in unison with superpopulation estimates (Table 4). The use of salmon availability as a covariate allows for the assessment of how yearly levels of salmon availability influence population trend and demography. However, the estimated relationships (Fig. 4) probably change as a function of density. For example, higher levels of salmon availability would potentially be needed to maintain λ levels near 1 when population sizes are higher. Density or population size could be used as a covariate to further explore this relationship (sensu Barker et al. 2002). Low sample sizes did not permit this analysis, but it may be possible once more years of data are collected.

Robustness of the Pradel model

It is likely that there is heterogeneity of capture probabilities with grizzly bear populations (Boulanger et al. 2002). Simulation studies have shown that estimates of λ from the Pradel model are robust to capture heterogeneity (Hines and Nichols 2002). The Pradel model is less robust to substantial change of capture probabilities of grizzly bears as a result of trap aversion or trap attraction (Hines and Nichols 2002). We doubt that behavior bias was present in our data given that our sampling procedure was passive and did not involve baiting the grizzly bears.

Sample size and model complexity limitations

Ideally, models that considered more complex river-specific demographic relationships could be considered in the mark–recapture analysis. However, the observed sample size of grizzly bears limited the complexity of models that could be considered with the data. In general, the number of parameters that can be estimated from a mark–recapture model is approximately the sample size of grizzly bears divided by 10 times the overdispersion parameter. Assuming the overdispersion parameter is equal to 1, then the approximate number of parameters that this analysis can support is 123 (the number of unique grizzly bears identified) divided by 10, which roughly equals 12. Models in Table 3 have 11–16 parameters and probably represent the maximal amount of complexity that the data set can support.

Comparison of the Pradel model estimates with helicopter survey count indices

Comparison of estimates of population trend from helicopter count block surveys of the entire Owikeno study area

and the Pradel model suggest agreement in terms of overall estimates of population trend. However, there was a disparity in 2001 on the Chuckwalla–Ambach sampling area survey where DNA-based superpopulation estimates and Pradel model λ estimates suggested an increase in grizzly bears, whereas count surveys suggested no increase (Table 4 and Fig. 4). One reason for this might be that helicopter counts only give point estimates of grizzly bears on salmon streams at one point in time compared with estimates of the cumulative superpopulation of grizzly bears estimated from DNA surveys (Table 4). Estimates of rates of addition (Fig. 4) suggested a large number of new grizzly bears in the Chuckwalla–Ambach sampling area in 2001. It is plausible that social factors such as territoriality around salmon resources limited the number of grizzly bears visible on salmon streams at any one time, leading to lower helicopter counts. However, many new grizzly bears potentially traversed the area during times in which helicopter surveys were not conducted, thus, leading to the larger number of grizzly bears identified (26; Table 2) and the positive population trend in grizzly bears in the Chuckwalla–Ambach sampling area (Fig. 4). In this case, we argue the DNA estimates of population trend and demography give a much clearer picture of the actual number of grizzly bears in the Chuckwalla–Ambach sampling area than helicopter counts. A key limitation of helicopter counts and other indices is that sightability of grizzly bears is assumed to be constant over time (Anderson 2001). Factor such as weather and social conditions limiting sightability in stream areas may cause this assumption to be violated, leading to potentially misleading results.

Comparison of the Pradel λ estimates with radiotelemetry λ estimates

Traditionally, most estimates of trend in grizzly bear populations have come from demographic projection of vital rate estimates obtained from radiotelemetry studies (Eberhardt et al. 1994; Hovey and McLellan 1996). Estimates of λ using the Pradel model include immigration and emigration to the area being sampled, whereas estimates of λ from radiotelemetry only consider birth and death processes. Given this, estimates of λ from DNA and radiotelemetry will only be equal if immigration and emigration from the study area is not occurring. As stated in Franklin (2001), λ estimates from radiotelemetry answer the question "Are individual replacing themselves?", whereas estimates of λ from the Pradel model answer the question "Are individuals being replaced?" The DNA-based estimate of population trend provides a more general picture of the status of the exact sampling area since the actual population size in the sampling area is influenced by immigration and emigration of grizzly bears. Estimates of population trend using radiotelemetry assume time-invariant life history parameters and λ, and a stable age distribution of grizzly bears (Boyce et al. 2001). In the case of our study, each of these assumptions is probably violated, which would most likely lead to biased and imprecise estimates of short-term population trend. However, a more intensive radiotelemetry study could provide estimates of true survival, reproductive rate, and causes of death that are not possible using DNA methods. Therefore, the optimal methodology to use for monitoring popula-

tions depends on exact research objectives and logistical constraints such as the viability of maintaining suitable sizes of radio-collared grizzly bears for time periods needed to estimate grizzly bear demographic parameters.

Comparison of N estimates with previous DNA N estimates

Previous DNA mark–recapture studies have all centered on the estimation of population size and density (Woods et al. 1999; Mowat and Strobeck 2000; Poole et al. 2001; Boulanger et al. 2002). A main sampling objective of these projects was to sample multiple synchronized sessions in a short duration of time to allow for the use of closed CAPTURE (Otis et al. 1978) models and accommodate the assumption of population closure. This usually involves the costly use of helicopters to allow quick access to remote sampling areas. In contrast, sampling for monitoring only requires one yearly session; data from multiple sampling sessions are pooled into one session. For this reason, sampling requirements are relaxed, thereby reducing the overall yearly cost of sampling. However, the same sites must be used on a yearly basis, and the study area must stay constant in size to meet the assumptions of the Pradel model (Franklin 2001).

The superpopulation size of grizzly bears using salmon streams was estimated with this data set using the methods of McDonald and Amstrup (2001). Estimation of density was not possible because of the fact that the actual area in which the grizzly bears were drawn from by the salmon streams was unknown. Given this, it was not possible to obtain an effective sampling area, and any population estimate can only be considered to be the cumulative number of grizzly bears that used salmon streams in the sampling areas during the fall sampling period. Population estimates using this method will be negatively biased because of the heterogeneity of capture probabilities (McDonald and Armstrup 2001); however, they do provide a useful way to interpret estimates of λ, as well as a conservative estimate of population size.

For determination of yearly population trend, we suggest that it is best to consider λ estimates from the Pradel model rather than the superpopulation estimates given the low precision of the superpopulation estimates in the beginning years of the study. For example, comparison of superpopulation estimates for the Neechanz–Genesee sampling area in 2000 and 2001 suggest that the population is stable (Table 4), whereas λ estimates for this year are greater than 1 (Fig. 4). However, this difference is probably due to the low precision of the 2001 superpopulation estimates as indicated by a CV of 60.3% (Table 4).

Conclusions

This study illustrates how the Pradel model can be used to provide estimates of population trend and valuable information about trends in population demography. We argue that this provides much more insight into causes of population trends than the use of count indices or similar methods. For example, with count indices it would be impossible to know whether changes in population size were due to arrival of new grizzly bears or the loss of grizzly bears from the study area. This study also suggests that the Pradel model and DNA sampling can be used as an alternative to more inten-

sive radio-collaring procedures in areas where logistics prohibit more intensive study. We argue that the multiple study-area design we used allows both exploration of heterogeneity in demographic trends between subpopulations, as well as enhanced precision for sparse data sets. Finally, this study illustrates the use of covariates to explore how changes in environmental conditions influence grizzly bear population demography and population trend.

Acknowledgements

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