ORIGINAL ARTICLE

WILEY Evolutionary Applications Open Access

A critical assessment of estimating census population size from genetic population size (or vice versa) in three fishes

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Abstract

Technological and methodological advances have facilitated the use of genetic data to infer census population size (N_c) in natural populations, particularly where traditional mark-and-recapture is challenging. The effective number of breeders (N_b) describes how many adults effectively contribute to a cohort and is often correlated with N_c. Predicting N_c from N_b or vice versa in species with overlapping generations has important implications for conservation by permitting (i) estimation of the more difficult to quantify variable and (ii) inferences of N_b/N_c relationships in related species lacking data. We quantitatively synthesized N_b/N_c relationships in three salmonid fishes where sufficient data have recently accumulated. Mixed-effects models were analysed in which each variable was included as a dependent variable or predictor term (N_b from N_c and vice versa). Species-dependent N_b/N_c slope estimates were significantly positive in two of three species. Variation in species slopes was likely due to varying life histories and reinforce caution when inferring N_b/N_c from taxonomically related species. Models provided maximum probable estimates for N_b and N_c for two species. However, study, population and year effects explained substantial amounts of variation (39%–57%). Consequently, prediction intervals were wide and included or were close to zero for all population sizes and species; model predictive utility was limited. Cost-benefit trade-offs when estimating N_b and/or N_c were also discussed using a real-world system example. Our findings based on salmonids suggest that no short cuts currently exist when estimating population size and researchers should focus on quantifying the variable of interest or be aware of caveats when inferring the desired variable because of cost or logistics. We caution that the salmonid species examined share life-history traits that may obscure relationships between N_b and N_c. Sufficient data on other taxa were unavailable; additional research examining N_b/N_c relationships in species with potentially relevant life-history trait differences (e.g., differing survival curves) is needed.

KEYWORDS
conservation biology, conservation genetics, effective population size, fisheries management, inventory and monitoring, wildlife management

1 | INTRODUCTION

Rapid technological and methodological advances in molecular genetics have increased interest in using genetic data to estimate or infer census population size (N_c), especially where counting individuals is challenging (e.g., in large populations, elusive species or extremely remote locations) (Baldigo, Sporn, George, & Ball, 2017; Fraser, Calvert, Bernatchez, & Coon, 2013; Guschanski et al., 2009; Luikart, Ryman, Tallmon, Schwartz, & Allendorf, 2010; Ovenden et al., 2016). While direct individual counts could be obtained from comprehensive genetic surveys (e.g., Guschanski et al., 2009), methodologies that indirectly estimate N_c from environmental DNA (eDNA) or subsamples of individuals from a population represent potentially cost-effective means through which census sizes could be estimated. Although eDNA is emerging as a potential method through which N_c could be inferred (Baldigo et al., 2017; Lacoursière-Roussel, Côté, Leclerc, Bernatchez, & Cadotte, 2016), its application for this purpose remains relatively novel. In comparison, the scientific literature examining methodologies for estimating the contemporary effective population size (N_e) of natural populations is relatively well developed.

The effective size of a population is a central evolutionary parameter influencing the extent of genetic drift, inbreeding and response to natural selection in isolated populations. Contemporary N_e (as opposed to long-term N_e, see Wang, 2005) represents a potentially useful tool to infer N_c because it can be linked specifically to recent cohorts and can be estimated from a (relatively) small number of genetic samples collected during a single collection event or over multiple temporal periods (Palstra & Fraser, 2012; Waples & Do, 2008). Understanding the conditions under which contemporary N_e (or its analogues) and N_c are associated with each other is highly valuable for conservation: it may be possible to use N_e to predict or monitor N_c (or vice versa) provided that relationships between N_e and N_c exist among or within populations and/or taxonomic groups (Bernos & Fraser, 2016; Ovenden et al., 2016; Tallmon et al., 2010; Whiteley et al., 2015).

For species with overlapping generations, the comparison of genetic and census population size can be made by comparing N_c to how many of those adults effectively contribute their genes to a single cohort, termed the effective number of breeders (N_b) (it should be noted, however, that this is dependent on the capacity to assign individuals to specific cohorts) (Waples & Do, 2010). With minimal life-history information, N_b can be used to infer contemporary N_e (Waples, Luikart, Faulkner, & Tallmon, 2013) and substitute for N_e when attempting to predict N_c. N_b also provides valuable insights into the eco-evolutionary dynamics of a population because interannual variation in N_b may be attributable to differences in individual adult reproductive success, family survival, and the overall number of families comprising the cohort (Waples & Antao, 2014; Whiteley et al., 2015).

Several recent studies have estimated N_b and N_c within multiple populations of the same species (e.g., Beebee, 2009; Bernos & Fraser, 2016; Ferchaud et al., 2016; Hoehn, Gruber, Sarre, Lange, & Henle, 2012; Perrier, April, Cote, Bernatchez, & Dionne, 2016; Whiteley et al., 2015). They identified important biological factors shaping N_b/N_c within species, such as habitat limitations, life-history traits or density dependence (Belmar-Lucero et al., 2012; Bernos & Fraser, 2016; Whiteley et al., 2013). Time series of N_b and N_c revealed that the two variables were positively correlated but that N_b/N_c was variable among populations and across years. Those results provided mixed support for the usefulness of one variable to infer the other in a monitoring context (Bernos & Fraser, 2016; Ferchaud et al., 2016; Whiteley et al., 2015). By comparison, few empirical investigations of the relationship between N_b and N_c among species have been conducted (Gomez-Uchida, Palstra, Knight, & Ruzzante, 2013; Osborne, Davenport, Hoagstrom, & Turner, 2010). Such comparisons would be extremely practical for determining how concordant N_b/N_c ratios are among taxonomically related species, an especially pertinent issue for rare species that lack data. It would also allow researchers to better understand factors contributing to variation in N_b/N_c in natural populations with contrasting biology or life history.

Most taxa still have little N_b/N_c data emerging, but sufficient data have become recently available in three fishes from the *Salmoninae* subfamily (Chinook salmon, Atlantic salmon and brook trout); these species form the basis of our quantitative analysis of N_b/N_c relationships. The studies examining these species have largely found positive relationships between N_b and N_c (e.g., Bernos & Fraser, 2016; Ferchaud et al., 2016; Perrier et al., 2016; Van Doornik, Waples, Baird, Moran, & Berntson, 2011; etc.); we collated data across studies to produce models for converting N_b to N_c (and vice versa) in each species. We then evaluated the efficacy of using one population variable to infer the other by generating population size parameter prediction intervals under which novel previously unsampled populations with only a single known population size variable (either N_b or N_c) are likely to fall. We also explored whether N_b/N_c curves differed for taxonomically related species and whether they could be used to infer population size parameters across species. Lastly, the monetary cost-benefit trade-offs of estimating N_b or N_c are discussed using a real-world example system in which N_b/N_c estimates were obtained across twelve populations.

2 | MATERIALS AND METHODS

2.1 | Primary Literature review

To find articles in which both N_b and N_c estimates were obtained for the same populations, keyword searches were conducted on the academic search engine ISI Web of Science™. A complete keyword search for "Effective number of breeders" was performed. Relevant references within retrieved studies were also searched for usable data. The goal of the analysis was to derive linear relationships between N_b and N_c across multiple species. A particular species was therefore only included in the final data set if a minimum of 10 total N_b/N_c estimates from at least three different populations were found; the only taxa with species for which these data requirement were satisfied were salmonids. A subsequent search of "Effective population size salmon*" was subsequently conducted to find any additional salmonid references missed by the initial search; this search found a single additional article. In most cases, N_c was "correctly linked" with brood year; that

is, each N_b estimate generated from a cohort was matched with the N_c estimate of the parental generation. Only in two cases were N_b and N_c incorrectly linked; these were estimates taken from populations in which N_c and N_b were estimated for the same year (i.e., researchers only sampled the population once). Both estimates were still included in the final data set.

Multiple methods exist to estimate N_b which make use of either linkage disequilibrium, heterozygote excess, molecular coancestry or sibship frequency information obtained from genetic markers (Wang, 2016). Although there is currently debate regarding which estimators perform best under a variety of scenarios (e.g., the violation of assumptions necessary for the linkage disequilibrium method such as random mating, no migration) (see Gilbert & Whitlock, 2015; Wang, 2016; Waples, 2016), the most commonly used estimator in our literature survey was the program LDNe (Waples & Do, 2008). This program makes use of linkage disequilibrium information to estimate N_e/N_b and is one of the most accurate programs currently available (Gilbert & Whitlock, 2015). Furthermore, Bernos & Fraser, 2016 included a comparison between Colony (which uses the sibship method) and LDNe and found a stronger link between N_b and N when the LDNe method was used. To reduce potential bias associated with different estimators and/or methods, only N_b estimates obtained from LDNe were therefore used.

One potential issue that emerged with using data obtained from LDNe was the inconsistent use across studies of critical *p*-value thresholds, which are used to exclude alleles with low frequencies from N_b estimation; low-frequency alleles can cause bias in N_b estimates (Waples & Do, 2010). This problem is most apparent at low sample sizes, which require higher critical *p*-values (Waples & Do, 2010); only N_b estimates derived from ≥30 samples were therefore retained (as in Johnstone, O'Connell, Palstra, & Ruzzante, 2012). Similarly, N_b estimates which included "infinity" as an upper confidence limit were excluded from the primary data set. When N_b and N_c estimates were contained in figures, the ImageJ program (Abràmoff, Magalhães, & Ram, 2005) was used to extract the data.

2.2 | Quantitative analysis

The efficacy of predicting both N_c from N_b and N_b from N_c was assessed using generalized linear mixed effect models (GLMMs). To generate models from which we could derive predictions, we evaluated the effect of N_b on N_c (and vice versa) across multiple species using the MCMCglmm package (Hadfield, 2010) in R (version 2.13.0; R Development Core Team, 2016) with a Poisson distribution and a log-link function given that census data represent counts of discrete individuals (as in Bernos & Fraser, 2016). MCMC chains were run for 1,000,000 iterations with a "burn in" period of 100,000 and thinning intervals of 50; the posterior distribution was therefore sampled > 10,000 times to obtain model parameters and associated 95% posterior density credible intervals (CI). Posterior traces and autocorrelation values were examined visually to evaluate and verify model convergence and mixing. The default (weakly informative) priors were used for all models.

Posterior modes for N_c or N_b were calculated from models in which N_b or N_c (respectively) was included as a continuous fixed effect and

"species" was included as a categorical fixed effect. An interaction between both fixed effects terms was also included. Population, study and year-within-study terms were included as random effects to account for issues of nonindependence in the data. The year random effect was nested within study except when studies were conducted by the same group of researchers on the same populations, in which case year was nested across the relevant studies. Heterogeneous variances for the residuals were specified using the *idh* function; residual error variance was allowed to differ for each level of the species variable.

As population size becomes large, it becomes increasingly difficult to confidently estimate Nb or Ne (Waples & Do, 2010). Models were also fitted that allowed us to explore whether residual variance changed with the fixed effect population size (N_b or N_c) variable. This was accomplished by fitting an observation-level random effect of the form "idh(species:sqrt(1/ln(N_x)):units" (when testing if variance decreased with the relevant population size variable, i.e., N_c or N_b) or "idh(species:sqrt(N_x)):units" (when testing if variance increased with the relevant population size variable) (as in Wood, Yates, & Fraser, 2016). Significance of this term was evaluated by comparing 95% CIs of N_x-related residual error estimates at five population sizes representative of the gradients present in our data set: 20, 50, 100, 300 and 600 for models predicting N_c from N_b, and 50, 100, 500, 1 000 and 10,000 for models predicting N_b from N_c. If CIs for the N_x-related residual variances overlapped between all representative population sizes, the heteroscedastic error term was subsequently removed.

Model performance was evaluated by calculating both marginal and conditional R^2 (Nakagawa & Schielzeth, 2013); slight modifications to the code described in the paper had to be made to accommodate the modelling of heterogeneous residual variances at the species level. Multiple R^2 values were computed for each model at the species level.

The efficacy and practicality of predicting N_c or N_b from a novel population (i.e., with random effects marginalized) was evaluated by examining 95% prediction intervals generated for each model across a gradient of N_c (when predicting N_b) or N_b (when predicting N_c). For most natural populations, N_b (or N_e) is almost always less than N_c (Kalinowski & Waples, 2002; Waples et al., 2013). Hence, when predicting N_b from N_c for natural populations, biologically meaningful and informative predicted values should typically fall within the predictor N_c value and 0. If upper N_b prediction interval values were greater than the predictor N_c values used to obtain them, the upper prediction intervals were considered fundamentally uninformative. When predicting N_b from N_c, lower 95% prediction interval values were considered "informative" only when they did not include (or were extremely close to) zero. When predicting N_c from N_b, meaningful predicted values could include any value greater than the predictor N_b value; both upper and lower prediction interval values were considered "informative" at a given size only when they were greater than the predictor N_b value used to obtain them.

A supplementary analysis was conducted that predicted N_c from the lower N_b CI reported in each paper as these are relevant for many conservation situations. Namely, when populations are difficult to sample effectively (i.e., populations are too large or individual samples are difficult to obtain), it can be challenging to obtain bounded

TABLE 1 Published studies examining N_b/N_c relationships among the three study species

Authors (Year)	Species	Number of Populations	Total N_b/N_c estimates
Johnstone et al. (2012)	*Salmo salar*	1	8
Palstra, O'Connell, and Ruzzante (2009)	*Salmo salar*	2	2
Perrier, Normandeau, Dionne, Richard, & Bernatchez, (2014)	*Salmo salar*	1	1
Perrier et al. (2016)	*Salmo salar*	9	23
Bernos et al. (In revision)[a]	*Salmo salar*	2	4
Ferchaud et al. (2016)	*Salmo salar*	9	19
Whiteley et al. (2015)	*Salvelinus fontinalis*	2	12
Bernos and Fraser (2016)	*Salvelinus fontinalis*	11	31
Ruzzante et al. (2016)	*Salvelinus fontinalis*	2	2
Van Doornik et al. (2011)	*Oncorhynchus tshawytscha*	5	15
Van Doornik et al. (2013)	*Oncorhynchus tshawytscha*	6	27
	Overall totals	40[b]	144

[a]See Appendix S1.

[b]Some populations were examined more than once across studies.

N_b point estimates, in which case lower CI may be more informative (Waples & Do, 2010). Using exclusively lower CI estimates allowed us to incorporate N_b estimates that had infinite upper CI, which increased the number of estimates in the data set by 42. However, prediction intervals calculated from N_b lower CI were always wider than models generated from point estimates (Figure S1); these models were therefore not reported.

3 | RESULTS

3.1 | Literature review

Of the 209 papers reviewed on N_b/N_c across taxa, 11 contained data that met inclusion criteria. The final data set contained 144 individual N_b/N_c estimates from 40 populations of three species: brook trout (15 populations), Atlantic salmon (14 populations) and Chinook salmon (11 populations) (Table 1). Any duplicate N_b/N_c estimates across studies on the same populations were removed from the data set. No other species had three or more populations for which N_b and N_c data had been estimated in adequate quantities (i.e., ≥10 data points total). N_b/N_c estimates for the three salmonid species included in this analysis were typically obtained across multiple years of sampling involving the genotyping of thousands of individuals; they represent the best data presently available in the literature for examining the predictive capacity of N_b to predict N_c (or vice versa).

3.2 | Predicting N_b from N_c

No evidence was found that residual error exhibited heteroscedasticity associated with N_c. Estimates of residual variance did not

TABLE 2 Between-species slope estimate contrasts and 95% credible intervals when predicting N_b from N_c and N_c from N_b

N_b from N_c		N_c from N_b	
Contrast	Estimate	Contrast	Estimate
AS vs CS	−0.336 (−0.658, −0.016)	AS vs CS	−0.518 (−0.895, −0.102)
AS vs BT	−0.269 (−0.510, 0.031)	AS vs BT	−0.488 (−0.945, −0.037)
BT vs CS	−0.066 (−0.377, 0.189)	BT vs CS	−0.127 (−0.557, 0.519)

AS, Atlantic salmon; CS, chinook salmon; BT, brook trout.

change with N_c; 95% CIs for residual error estimates overlapped for all population size ranges compared (Appendix S2). The heteroscedastic error term was therefore dropped from all subsequent analyses.

The slope of the relationship predicting N_b from N_c differed significantly between some species. Slope estimates were significantly or marginally lower for Atlantic salmon relative to Chinook salmon (P_{mcmc} = 0.0413, Table 2) and brook trout (P_{mcmc} = 0.076, Table 2), respectively; 95% CIs for estimated differences barely overlapped zero. The slope of the relationship predicting N_b from N_c differed marginally from zero for Atlantic salmon (P_{mcmc} = 0.078, Table 3, Figure 1), whereas posterior mode slope estimates for brook trout and Chinook salmon were significant and positive with CIs not overlapping zero (P_{mcmc} < 0.001 and P_{mcmc} < 0.001, Table 3, Figure 1). Slope estimates did not differ between brook trout and Chinook salmon (P_{mcmc} = 0.563, Table 2).

TABLE 3 Slope and intercept estimates with 95% credible intervals for models predicting N_b from N_c and N_c from N_b for three salmonid species

| Species	Intercept	Slope	Marginal R^2	Conditional R^2
N_b from N_c				
Atlantic salmon	3.705 (2.335, 5.266)	0.195 (−0.029, 0.429)	0.424	0.857
Brook trout	0.932 (−0.329, 2.480)	0.449 (0.278, 0.611)	0.394	0.865
Chinook salmon	1.200 (−0.411, 2.761)	0.528 (0.303, 0.765)	0.343	0.737
N_c from N_b				
Atlantic salmon	5.821 (4.655, 7.013)	0.067 (−0.141, 0.272)	0.376	0.941
Brook trout	4.932 (2.824, 6.449)	0.590 (0.133, 0.976)	0.376	0.902
Chinook salmon	2.992 (1.537, 4.527)	0.558 (0.236, 0.902)	0.321	0.856
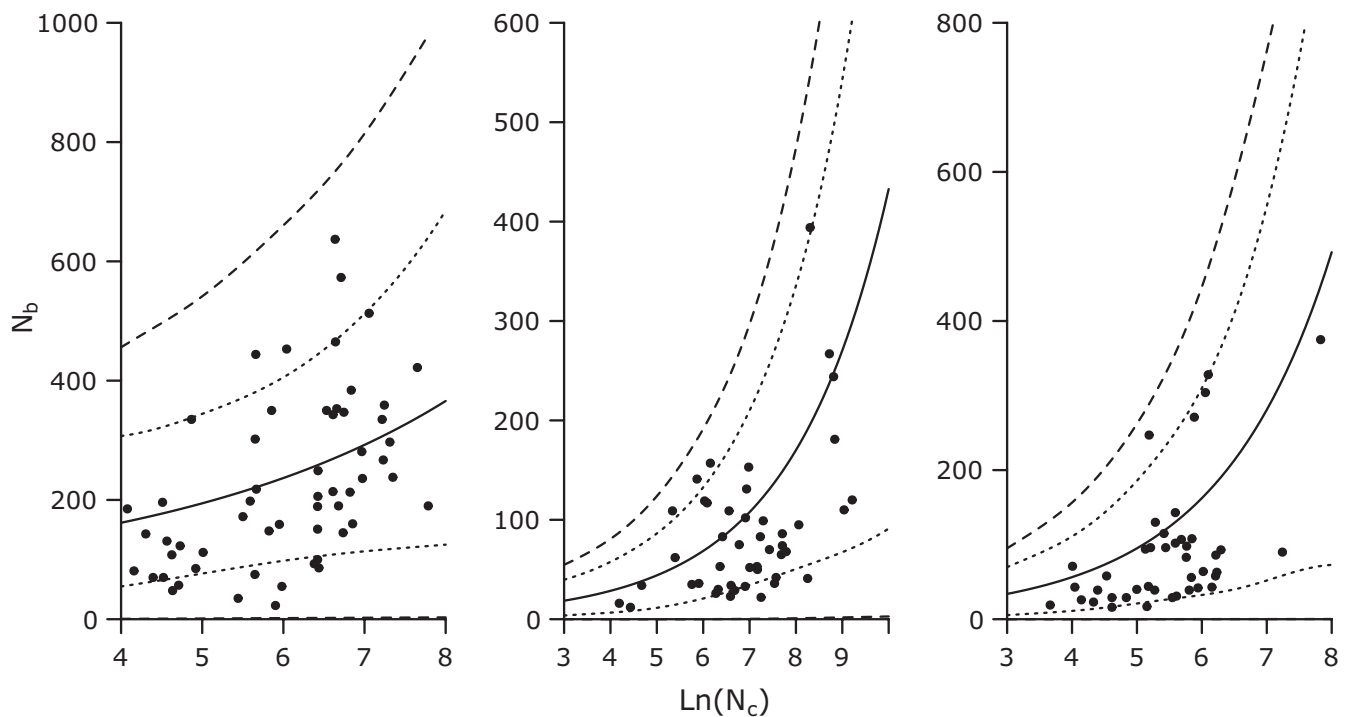
FIGURE 1 Relationship predicting N_b from N_c in Atlantic salmon (a), brook trout (b) and Chinook salmon (c). Dotted lines represent 95% credible intervals; dashed lines represent 95% prediction intervals

The N_c and species terms accounted for 34%–42% of the variation present in the data, depending on species; the population, study and year random effects terms accounted for 39%–47% of the variation (Table 3).

Prediction intervals for Atlantic salmon were uninformative as a result of a lack of a significant relationship predicting N_b from N_c (i.e., slope estimate CIs overlapped zero). Lower 95% prediction intervals for brook trout and Chinook salmon were uninformative; they included (or were extremely close to) zero for both species (Figure 1). Upper 95% prediction interval values were informative for most N_c values for brook trout: upper N_b prediction intervals were lower than predictor N_c values for census sizes greater than approximately 100 individuals.

Chinook salmon upper prediction interval values were meaningful only for large N_c values; upper 95% prediction interval values were lower than predictor N_c values for census sizes greater than approximately 650 individuals.

3.3 | Predicting N_c from N_b

No evidence was found that residual error exhibited heteroscedasticity associated with N_b. The CIs for residual error estimates also overlapped for all population size ranges compared (Appendix S2). The heteroscedastic error term was therefore dropped from all subsequent analyses.
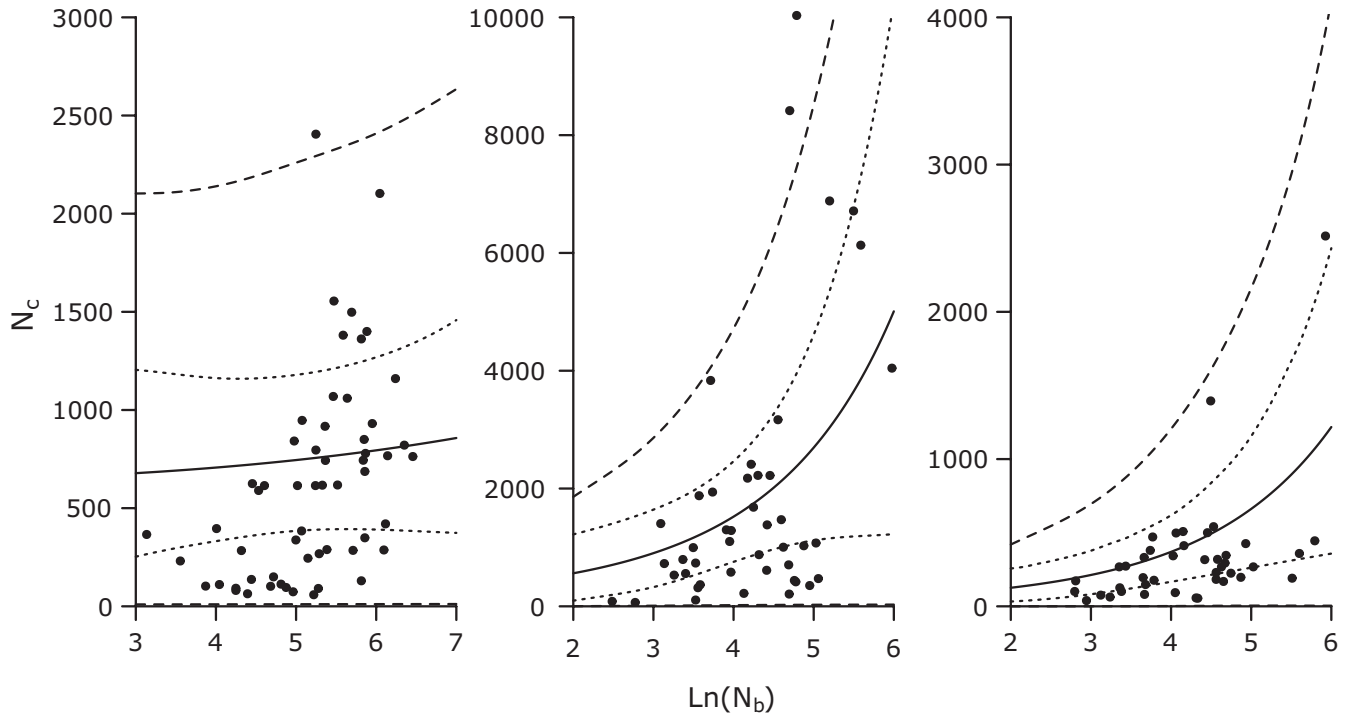
FIGURE 2 Relationship predicting N_c from N_b in Atlantic salmon (a), brook trout (b) and Chinook salmon (c). Dotted lines represent 95% credible intervals; dashed lines represent 95% prediction intervals

The slope of the relationship predicting N_c from N_b also differed significantly between some species. The slope estimates for Atlantic salmon were significantly lower than for Chinook salmon (P_{mcmc} = 0.011, Table 2) and brook trout (P_{mcmc} = 0.031, Table 2). The slope of the relationship predicting N_c from N_b did not differ from zero for Atlantic salmon (P_{mcmc} = 0.550, Table 3, Figure 2). Posterior mode slope estimates for both brook trout and Chinook salmon were again significantly positive, and CIs did not overlap zero (P_{mcmc} = 0.009 and P_{mcmc} = 0.001, Table 3, Figure 2); slope estimates also did not differ between brook trout and Chinook salmon (P_{mcmc} = 0.941, Table 2).

The N_b and species terms accounted for 32%–38% of the variation present in the data, depending on species; the population, study and year random effects terms accounted for 53%–57% of the variation.

Prediction intervals for Atlantic salmon were uninformative as a result of a lack of a significant relationship predicting N_c from N_b (i.e., slope estimate CIs overlapped zero). Lower 95% prediction intervals for brook trout and Chinook salmon were uninformative; they included (or were extremely close to) zero for both species (Figure 2). Upper 95% prediction interval values were meaningful for all N_c values for both species: upper prediction intervals for N_c were always greater than predictor N_b values for all population sizes.

4 | DISCUSSION

4.1 | Using N_c to predict N_b or using N_b to predict N_c

Recent studies have suggested that N_b and N_c were correlated among intraspecific populations and that one could be used to predict the other

if N_b/N_c relationships were well characterized for a particular species (Bernos & Fraser, 2016; Ferchaud et al., 2016; Osborne et al., 2010). To formally test this hypothesis, we modelled the relationship between N_b and N_c using a database of 40 populations from three salmonid fishes and generated prediction intervals using those models to determine efficacy of predicting one population size variable from the other. The 95% prediction intervals for some species provided potential maximum thresholds for some population size variables. For example, a brook trout population with an N_c of approximately 1,000 is not likely to have an N_b higher than 300. However, the practical usefulness of this upper threshold varies depending on the species and the estimated variable.

Brook trout and Chinook salmon had potentially informative and biologically meaningful upper prediction intervals for N_c when predicted from N_b. Upper prediction thresholds, however, were up to almost two orders of magnitude larger than the predictor N_b values, placing them on the extreme end of N_b/N_c ratios documented in wild salmonid populations (Palstra & Fraser, 2012). Furthermore, while "informative" upper thresholds for N_b can be predicted from moderate and large N_c values for brook trout and Chinook salmon, these thresholds may not be informative from a practical management standpoint because, from a conservation genetics standpoint, N_e is often the variable of more interest. Both N_e and N_b are likely to be less than N_c in natural populations (Waples et al., 2013); the criteria for biologically meaningful predicted N_b values would, however, be even more stringent when translating predicted N_b values to N_e values given that N_b is typically less than N_e. N_b in brook trout, for example, can range from 0.34 to 0.68 of N_e, depending on the conversion methodology used (Bernos & Fraser, 2016).

It is also unsurprising that N_b upper prediction interval values overlapped with predictor N_c values at small N_c in brook trout and small-to-moderate N_c in Chinook salmon; as N_c increases, the N_b/N_c ratio tends to decrease because of density-dependent effects on reproduction (Bernos & Fraser, 2016; Ferchaud et al., 2016; Whiteley et al., 2015). The models also did not accurately provide minimum prediction thresholds for both population size variables; for all species, lower prediction intervals at all N_b or N_c sizes either included or were extremely close to zero across all population sizes examined.

Recent empirical studies have shown that changes in N_b do not always track changes in N_c within a population over time (Bernos & Fraser, 2016). Primary studies also reported that spatial variation among populations in N_b/N_c ratios was approximately twofold greater than temporal variation within populations for two of the three species in our synthesis (Bernos & Fraser, 2016; Ferchaud et al., 2016). Similarly, study, population and year level random effects accounted for substantial amounts of variation in our analysis (between 39%–57%). This variability in N_b/N_c is likely a result of several biological processes acting differentially and simultaneously within and among populations, including the degree of population connectivity (Fraser, Lippé, & Bernatchez, 2004; Gomez-Uchida et al., 2013; Lamy, Pointier, Jarne, & David, 2012), environmental conditions (Bernos & Fraser, 2016; Whiteley et al., 2015) or ecological differences (Belmar-Lucero et al., 2012; Waples et al., 2013). Such population variability present in both N_b and N_c measurements probably affected the accuracy and precision of predictions, limiting the utility of the models for predicting N_b or N_c for novel, nonsampled populations.

4.2 | Relationship between N_b and N_c among three salmonid species

Another primary study objective was to assess whether the trajectory and magnitude of the relationship between N_b and N_c differed among taxonomically related species; our results provide mixed support for this at the Salmoninae subfamily level. A general positive correlation between N_b and N_c was observed in brook trout and Chinook salmon: larger populations tend to have larger N_b. However, the slope estimates for Atlantic salmon predicting N_c from N_b or N_b from N_c were either not significantly different from zero or only marginally different from zero. Therefore, (i) taxonomically related species should not be assumed to exhibit similar N_b/N_c ratios; and (ii) ecological and life-history characteristics of naturally spawning Atlantic salmon could buffer small populations against a loss of genetic diversity.

Reproductive life histories differ markedly among salmonids. While male brook trout exhibit variable ages at maturity (Hutchings, 1993) and male Chinook salmon exhibit alternative reproductive phenotypes (Berejikian et al., 2010), male Atlantic salmon exhibit one of two extreme reproductive phenotypes: an early maturing freshwater phenotype (1–2 years of age) or an anadromous phenotype (typically 4–6 years of age) (Hutchings & Jones, 1998; Myers, Hutchings, & Gibson, 1986). In some populations, up to 80% of males delay or forgo oceanic migration to mature in freshwater (Myers et al., 1986) at a size much smaller than their anadromous conspecifics (Hutchings & Myers, 1988). The presence of the early maturation phenotype is well known to have a positive influence on N_e by balancing sex ratios, decreasing variance in reproductive success and increasing outbreeding between cohorts within a population (Johnstone et al., 2012; Jones & Hutchings, 2001; Perrier et al., 2014; Saura, Caballero, Caballero, & Morán, 2008).

The primary literature N_c estimates excluded early maturation phenotypes ("parr") in all but two (landlocked) Atlantic salmon populations. Most N_c estimates are actually estimates of anadromous adults only and therefore underestimate the number of reproductive individuals within a population (Myers, 1984; Perrier et al., 2014). This very likely explains the lack of relationship between N_c and N_b for Atlantic salmon; observed N_b/N_c ratios are probably upwardly biased because the male alternative phenotype may buffer N_b estimates when male anadromous numbers are small (Ferchaud et al., 2016; Johnstone et al., 2012). Future research on any species should include all reproductive phenotypes when estimating N_c.

N_b/N_c relationships were similar in brook trout and Chinook salmon, with N_b tending to increase at a similar rate with N_c. These species have substantial differences in life histories (e.g., semelparity vs. iteroparity, obligate vs. facultative anadromy), but their spawning behaviour can be similar. Both, for example, prefer spawning habitat with hypoheic upwelling (Curry & Noakes, 1995; Geist, 2000; Geist & Dauble, 1998) and spawn at high densities; brook trout have been observed to exhibit aggregate spawning (Belmar-Lucero et al., 2012; Blanchfield & Ridgway, 1997) and Chinook salmon spawn in clusters at densities much higher than Atlantic salmon (Fleming, 1998; Geist & Dauble, 1998). As N_c increases within populations in both species similar density-dependent issues may emerge (i.e., mate competition, nest superimposition) and affect N_b.

Overall, the among species comparisons suggest that extrapolating N_b or N_c estimates from N_b/N_c curves for species related at the family/subfamily taxonomic level may, in some cases, over- or underestimate population size estimates; mixed evidence was found that N_b/N_c relationships differed between these species, with observed differences likely a result of different species-level life-history characteristics. If N_b/N_c relationships for a taxonomically related species are used as "proxy" population parameters for another "data-deficient" species, careful consideration should be taken to evaluate life-history and behavioural similarities to determine whether such an extrapolation is valid or meaningful.

4.3 | Cost-benefit consideration in quantifying N_b or N_c to infer the other

Conservation resources are often limited; it is therefore important to consider the relative costs of quantifying N_c and N_b in wild populations given the degree of uncertainty in converting one to the other. To help other researchers considering similar research projects, we provided an example of the comparative costs of estimating N_c and N_b in a series of stream brook trout populations of varying size from Cape Race, Newfoundland, Canada (Table 4). This was based on one of the largest empirical studies of N_b/N_c to date (Bernos & Fraser, 2016; see Table 1). Intriguingly, the relative costs of quantifying N_c

	Small population	**Medium population**	**Large population**
Expense	N_c = 50–500	N_c = 500–1,500	N_c = 1500–10000
N_c estimation from mark–recapture			
Field labour (person days)	$180 (1.2)	$360 (2.4)	$600 (4.0)
Equipment use and maintenance demands	$35	$50	$95
Office labour (person days)	$20 (0.13)	$20 (0.13)	$20 (0.13)
Miscellaneous field expenses[a]	$200	$225	$715
Total cost, N_c estimation	$435	$655	$1,460
N_b estimation using molecular markers			
Field labour (person days)	$75 (0.5)	$150 (1.0)	$225 (1.5)
Equipment use and maintenance demands	$65	$110	$150
Molecular laboratory and office labour (person days)	$180 (1.20)	$255 (1.70)	$330 (2.20)
Molecular consumables[b]	$240	$440	$640
Total cost, N_b estimation	$560	$955	$1345

TABLE 4 Example cost-benefit trade-offs associated with estimating N_c and N_b in wild populations, based on one of the largest N_b/N_c studies to date conducted on brook trout occupying small streams in Cape Race, Newfoundland, Canada (Bernos & Fraser, 2016). Expenses are approximate and in CDN dollars

[a]Does not include travel expenses to/from field site (gas/food/accommodation), nor travel expenses for the marking event (these would be equivalent for N_b and N_c estimation).
[b]Based on 10–15 microsatellite loci, and sample sizes of n = 35, 65, and 95 for small, medium and large populations, respectively.

and N_b were very similar. Costs unsurprisingly increased with increasing population size: in general, more labour resources were required to estimate N_c and more consumables were required to estimate N_b using molecular markers. Given this, the choice of estimating N_c or N_b may depend largely on how much confidence one desires in estimating either variable specifically while balancing other considerations. For example, at Cape Race estimating N_c with accuracy and precision is feasible but can be invasive, requiring the tagging of many adults within streams (especially for large populations). Conversely, estimating N_b is arguably less invasive in relying on sampling juvenile cohorts that naturally experience density dependence, but these N_b estimates may only translate into maximum estimates of N_c.

4.4 | Future research

The number of populations with data available for each species in our models was modest (11–15 per species, limited to the *Salmoninae* sub-family). The species examined in this study (salmonids) may share life-history traits that could potentially obscure the relationship between Nb and Nc. Salmonids, for example, are characterized by type-III survival curves; species with high fecundity and juvenile mortality typically exhibit low N_e/N_c ratios (Palstra & Ruzzante, 2008). The salmonid species examined also exhibit high variance in reproductive success (Blanchfield,

Ridgway, & Wilson, 2003; Tentelier et al., 2016). Relationships between N_b and N_c for species with higher N_b/N_c ratios or lower variance in N_b over time could be stronger. This review examined data for all taxa, but sufficient data were available only for species from the Salmoninae sub-family; unfortunately, the data necessary to examine N_b/N_c relationships among other taxonomic groups with differing life-history characteristics are not available in the scientific literature at this time.

While several other species (both salmonid and nonsalmonid) did have studies in which both N_b and N_c were estimated (see Appendix S3) they were excluded from our final data set for three reasons: (i) population size variables were only estimated for one or two populations across studies in each species; (ii) adequate data did not exist to generate robust species curves (i.e., ≥10 datapoints); or (iii) LDNe was not used to obtain N_b estimates. As further studies examine N_b/N_c relationships within a variety of taxa, it may be possible to generate more robust predictive models and increase their practical utility for conservation purposes.

This study focused partially on the practicality of predicting N_b or N_c for novel, previously unsampled populations based on relationships generated from recently published data. While these predictive models were somewhat limited in their practical applications, it may still be possible to use these models to reliably infer one population size variable from the other for populations with well-established

baseline data. Population and temporal model terms often account for a significant component of the variation observed in population size terms (Ferchaud et al., 2016); with enough temporal data, it may be possible to reliably track changes in one population size variable through the other (but see Bernos & Fraser, 2016). Although outside the scope of this study, future research could examine under what conditions this could be reliably carried out. For example, how many years of historical data are necessary to reliably track a given population? Are N_b/N_c relationships in some species more variable over time than others? Are certain ecological or life-history traits among populations associated with more stable N_b/N_c relationships?

The extent to which the N_b/N_c relationships explored herein apply to differing ecotypes of the explored species is also unknown. Salmonids are an extremely plastic taxa; many species have multiple life-histories and/or inhabit a wide range of habitats. The brook trout populations represented in this study, for example, are largely lentic; whether the modelled N_b/N_c relationships could be extrapolated to lotic or anadromous populations remains undetermined.

Finally, we found no evidence for heteroscedasticity in any of the modelled N_b/N_c relationships, although there have been indications of this across population size gradients in studies with a large number of populations (Bernos & Fraser, 2016). Therefore, future studies are encouraged to continue to account for this potential heteroscedasticity, particularly given that it becomes increasingly difficult to estimate genetic population size variables (N_b, N_e) for large populations (Waples & Do, 2010).

5 | CONCLUSIONS

Although estimating the maximum number of adults present in a given population could help guide management and conservation decisions, the upper prediction intervals determined herein generally represented documented taxonomic extremes for N_b/N_c ratios in salmonids and lower prediction intervals were largely uninformative; predicting a precise N_b or N_c estimate for a novel population based off of a single population size variable is, with current data available, not realistically possible. While N_c prediction intervals generated from N_b estimates were marginally worse than prediction intervals in salmonids generated from other molecular data (e.g., eDNA in Baldigo et al., 2017), realizing the full potential of the anticipated conservation applications of genetic techniques to predict and estimate N_c (e.g., Luikart et al., 2010) will realistically require the accumulation of more data.

Molecular technologies and methods are rapidly advancing and could represent a practical means of estimating N_c in the future. However, researchers should be cognizant of the limitations of using one population size variable to infer the other; researchers and/or managers should, whenever possible, focus efforts on quantifying the population size variable of interest except when the costs/logistics of measuring that variable are prohibitive. Further research is also necessary to determine whether less variable relationships exist between N_b and N_c for other taxonomic groups with differing life-history characteristics than salmonids.

DATA ARCHIVING STATEMENT

Data for this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.136bm.

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