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# Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life-history forms

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## Abstract

The effective population size is influenced by many biological factors in natural populations. To evaluate their relative importance, we estimated the effective number of breeders per year ( $N_b$ ) and effective population size per generation ( $N_e$ ) in anadromous steelhead trout (*Oncorhynchus mykiss*) in the Hood River, Oregon (USA). Using demographic data and genetic parentage analysis on an almost complete sample of all adults that returned to the river over 15 years (> 15 000 individuals), we estimated  $N_b$  for 13 run years and  $N_e$  for three entire generations. The results are as follows: (i) the ratio of  $N_e$  to the estimated census population size ( $N$ ) was 0.17–0.40, with large variance in reproductive success among individuals being the primary cause of the reduction in  $N_e/N$ ; (ii) fish from a traditional hatchery program ( $H_{\text{trad}}$ : nonlocal, multiple generations in a hatchery) had negative effects on  $N_b$ , not only by reducing mean reproductive success but also by increasing variance in reproductive success among breeding parents, whereas no sign of such effects was found in fish from supplementation hatchery programs ( $H_{\text{supp}}$ : local, single generation in a hatchery); and (iii)  $N_b$  was relatively stable among run years, despite the widely fluctuating annual run sizes of anadromous adults. We found high levels of reproductive contribution of non-anadromous parents to anadromous offspring when anadromous run size is small, suggesting a genetic compensation between life-history forms (anadromous and nonanadromous). This is the first study showing that reproductive interaction between different life-history forms can buffer the genetic impact of fluctuating census size on  $N_e$ .

*Keywords:* effective population size, genetic compensation, microsatellite, *Oncorhynchus mykiss*, parentage analysis, salmonid

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## Introduction

The effective population size ( $N_e$ ) is one of the most important parameters in evolutionary and conservation biology, not only because  $N_e$  determines the degree of genetic drift and the effectiveness of natural selection, but also because it affects population viability (Frankham *et al.*

2002; Hedrick 2005a). However, this parameter is also one of the most difficult to estimate in natural populations. Many factors influence  $N_e$  including sex ratio, variance in family size among individuals, fluctuations in population size, and age structure (Crow & Kimura 1970). As a consequence,  $N_e$  is often much less than the census size ( $N$ ) in many species (e.g. Husband & Barrett 1992; Scribner *et al.* 1997; Turner *et al.* 2002). Because  $N$  is generally much easier to measure than  $N_e$ , there has been much interest in predicting  $N_e/N$  ratios, particularly for conservation applications (Frankham 1995a, 2002). However, how best to measure  $N_e/N$  ratios, and whether they are constrained within a narrow range in nature or can take extremely low values

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for some species, remain open questions (Nunney 1993, 1995; Frankham 1995b; Hauser *et al.* 2002; Kalinowski & Waples 2002; Hedrick 2005b). In addition, the factors that can reduce  $N_e/N$  ratios usually act simultaneously, which makes it difficult to distinguish their individual effects. As a consequence, few empirical studies have addressed the relative importance of the different factors above in reducing  $N_e/N$  in natural populations (Frankham 1995b; Storz *et al.* 2002; Ardren & Kapuscinski 2003).

Two additional factors may affect  $N_e$  and  $N_e/N$  in practice. One is artificial propagation, in which natural populations are supplemented with cultured individuals. Artificial propagation is common for economically valuable species (Leber 2004), but many conservation programs also utilize artificial propagation to support natural populations of endangered species (Cuenco *et al.* 1993; Olney *et al.* 1994). These species now include many hundreds of taxa in both aquatic and terrestrial systems (Frankham 2002). Although the effects of artificial propagation on  $N_e$  in natural populations have been evaluated theoretically (Ryman & Laikre 1991; Waples & Do 1994; Wang & Ryman 2001; Duchesne & Bernatchez 2002), empirical data on this important topic are limited (Ballou & Foose 1996; Hedrick *et al.* 2000; Gautschi *et al.* 2003).

Another potential factor that can affect  $N_e$  and  $N_e/N$  is life history polymorphisms (e.g. behavioural polymorphisms such as resident and migratory forms, and alternative mating strategies such as dominant males vs. sneaker males). Different life-history forms can have different reproductive success in different circumstances, and interbreeding between life-history forms might buffer fluctuations in  $N_e$  in some circumstances. For example, if abundance of one life-history form fluctuates widely, while that of the other form is relatively stable, then overall  $N_e$  will be stabilized through time by interbreeding between forms. Similarly, if the sex ratio of one form is heavily skewed the overall sex ratio (and hence  $N_e$ ) can be balanced by interbreeding between life-history forms. This topic is just beginning to be studied in detail, but already it is clear that the relative contributions of different life-history forms can have important consequences for effective population size (Martinez *et al.* 2000; Garcia-Vazquez *et al.* 2001). Parallel situations occur in many marine fish species that have sex reversal (Muñoz & Warner 2003) and in a variety of species (from insects to mammals) that have dominant and sneaker males (Wade & Shuster 2004).

Salmonid species provide a good model system for evaluating  $N_e$  and  $N_e/N$  ratios. Salmonids are of considerable economic, social, and cultural interest, and they spawn at predictable times in discrete freshwater populations. As a result, these species have been well studied and census population sizes can often be estimated very accurately. Anadromous Pacific salmonids (*Oncorhynchus* spp.) are also semelparous, or nearly so, which facilitates conversion

of estimates of the effective number of breeders per year ( $N_b$ ) into effective size per generation ( $N_e$ ) (Waples 2002a). These life history traits — semelparity with variable age at maturity — are shared by a number of other taxa, including many monocarpic plants and crustaceans with diapausing eggs (Waples 2006a). Genetic data have long been used in the conservation and management of salmonid populations, so a large number of markers are available for estimating effective size and  $N_e/N$  ratios using genetic data (Hedrick *et al.* 2000; Heath *et al.* 2002; Ardren & Kapuscinski 2003; Waples 2004).

*Oncorhynchus mykiss* has two distinct life-history forms: steelhead trout, which are anadromous, and resident rainbow trout, which stay in freshwater throughout the life cycle (hence nonanadromous). Despite frequent interbreeding between anadromous and nonanadromous fish in natural populations (Zimmerman & Reeves 2000; Salmon Recovery Science Review Panel 2004), the influence of this interbreeding on  $N_e$  has never been studied. In a previous study, we found large fluctuations in the numbers of returning adults among years, low reproductive success of adult fish from a traditional hatchery program in the wild, and a large reproductive contribution of nonanadromous fish to anadromous populations in steelhead populations in the Hood River, Oregon (Araki *et al.* 2006). Thus, this system is ideal for evaluating the effect of interbreeding between different life-history forms on  $N_b$  and  $N_e$ .

In this study, we use demographic data and microsatellite-based parentage assignments to estimate  $N_b$  and  $N_e$  in two steelhead populations (summer run and winter run) in the Hood River. Our data set includes more than 15 000 samples, representing almost all (>97%) anadromous adults that returned to spawn in the river between 1991 and 2003. We investigate 13 run years of parents and their offspring (that returned to the river as adults in subsequent run years), which covers one full generation of summer run and two full generations of winter run. We address: (i)  $N_e/N$  ratios in these populations and the influence of various factors that affect  $N_b$  and  $N_e$  (sex ratio, variance in reproductive success among individuals, temporal variation in reproductive success) on  $N_e/N$ ; (ii) the effects of hatchery propagations on  $N_b$  and  $N_e$ ; and (iii) temporal fluctuation (or stability) of  $N_b$  and its cause in the natural populations. This is the first study to estimate  $N_e$  directly from almost complete demographic data for entire generations of anadromous populations of a salmonid. Although we do not have nonanadromous samples, the almost complete sampling from anadromous steelhead and the parentage analysis allow us to infer the relative contribution of nonanadromous parents to the anadromous populations.

## Materials and methods

See Table 1 for an explanation of notation.

**Table 1** Notation used in this paper

$N_e$	Effective population size per generation
$N_b$	Effective number of breeders per run year
$N_{\text{anad}}$	Number of anadromous fish passed above the dam each run year; this includes both hatchery-born and wild-born fish
$N$	Total number of potential parents, including anadromous and nonanadromous parents
$\hat{N}$	Estimate of $N$ based on equations 1 and 2
$\bar{k}$	Mean reproductive success (family size) among parents
$V_k$	Variance in reproductive success (family size) among parents
$V_k/\bar{k}$	Index of variability (= variance in reproductive success divided by mean reproductive success)
	'Adjusted $V_k/\bar{k}$ ' means using $\bar{k}$ adjusted for the bias that results from parentage assignment errors (via equation 3)
	'Scaled $V_k/\bar{k}$ ' means scaled to a stable population size of $\bar{k} = 2$ (also via equation 3)
	This scaling allows one to compare the index of variability among different datasets
$H_{\text{trad}}$	Fish from the traditional hatchery program using nonlocal brood stock that reared multiple generations in hatcheries
$H_{\text{supp}}$	Fish from the supplementation hatchery program using local, wild brood stock

### Study populations

The Hood River basin is a tributary of the Columbia River in the Northwest United States. Since 1991 almost every adult steelhead returning to spawn in this river has been catalogued, measured, and had scale and fin-snip samples taken (for DNA analysis) at the Powerdale Dam fish trap by staff of the Oregon Department of Fish and Wildlife (ODFW). This dam is located 4.0 river miles from the mouth of the Hood River. Steelhead only spawn above the dam, which is a complete upstream barrier to migration for all salmonids. The year in which each returning adult was born (brood year) was determined via scale reading, and the average generation time (birth-year of parents to birth-year of offspring) was estimated as 5.2 years for summer runs and 4.3 years for winter runs. Although there is some overlap in the run timing of the two populations (summer run: April to October, winter run: January to June Kostow 2004), summer run and winter run fish are usually quite distinguishable because they only overlap in run timing for a brief period, and during this time winter run are sexually mature and summer run are not. Both runs breed in the spring, but in different forks of the river. Fewer hybridization events between populations were identified in our parentage analysis than the number of matches expected by chance alone given our empirical estimates of assignment error rates (i.e. type-B error rates, see below), indicating there is little or no hybridization between the two run populations. Indeed, microsatellite-based  $F_{\text{ST}}$  between run populations was 0.009, nearly 10 times higher than temporal  $F$  among run years within populations ( $F = 0.001$ ) (Hedrick 2005a). Steelhead is an iteroparous species (repeated reproductive bouts possible), but we treated all the fish as semelparous (only one reproductive bout in a lifetime) because the proportion of repeat spawners is very low in this river (< 5%).

In a previous study on the Hood River (Araki *et al.* 2006), we found that a large fraction of anadromous fish did

not have one or both parents among the anadromous spawners from the year in which they were born. Here we call these missing parents 'nonanadromous parents', because we have almost complete samples from anadromous parents for the run years we examined. We believe that the majority of the missing parents are resident trout, which are common in the Hood River (Olsen 2003). Precocious parr (presmolts that mate before going to sea) might also be involved, but they have not been widely reported in steelhead. Strays from other rivers could also explain the missing parents. However, we believe that strays are not a major source of the missing parents in this river for the following reasons: (i) a large proportion of offspring had at least one parent from the Hood River (Araki *et al.* 2006); (ii) offspring with both parents missing (potential strays) are genetically indistinguishable to offspring whose parents are in the sample (unpublished data); and (iii) according to the hatchery-born fish identification, the straying rate from other rivers to the Hood River is low (2%–3%; E. Olsen, personal communication).

For parents, the run year is the year in which adult fish begin arriving at the river to spawn, and is the calendar year before they actually spawn. Hence fish from the 1995 run year began arriving in 1995 and spawned in the spring of 1996 (which is the brood year of their offspring). In this study, we investigated five consecutive run-year samples of summer run (run years 1994–98; hereafter Su94 to Su98) that roughly cover one complete generation in the summer-run population, and eight consecutive run-year samples of winter run (run years 1991–98; hereafter Wi91 to Wi98) that roughly cover two consecutive generations in the winter-run population. The adult samples that returned to the river between run year 1994 and 2003 for winter run and between run year 1998–2003 for summer run were used as offspring samples, based on their brood years. Because our samples cover more than one generation, some samples were used both as offspring samples (in earlier sample sets) and as parent samples (in later sample sets). The total

**Table 2** Number of anadromous parents and their offspring cohorts returned to the Hood River

Run year	Parents			Offspring	
	$N_{\text{anad}}$	%Wild	%Male	$N_{\text{Offspring}}$	$N_{\text{Offspring}}/N_{\text{anad}}$
Summer run (Su)					
Su94	1831	10.3	40.8	198	0.11
Su95	650	20.3	39.7	208	0.32
Su96	1486	12.2	37.5	588	0.40
Su97	529	15.7	33.5	456	0.86
Su98	136	97.1	27.9	240	1.76
Su total	4632	15.5	38.4	1690	0.36
Winter run (Wi)					
Wi91	1008	71.0	46.3	271	0.27
Wi92	412	98.8	38.6	303	0.74
Wi93	384	99.5	32.6	212	0.55
Wi94	208	97.1	50.0	296	1.42
Wi95	461	59.9	47.5	1233	2.67
Wi96	572	50.7	40.4	983	1.72
Wi97	422	52.8	37.2	879	2.08
Wi98	517	57.4	42.2	612	1.18
Wi total	3984	70.1	42.2	4789	1.20

$N_{\text{anad}}$  represents a number of anadromous steelhead adults returned to the Hood River and passed above the dam (complete upstream barrier to the spawning grounds), and  $N_{\text{Offspring}}$  represents a number of anadromous steelhead adults that were born in the wild in the year when corresponding parental adults spawned, and that returned to the Hood River in the subsequent run years (mostly as 2–6 years old). We identified the brood years of returning offspring by ageing their scales. %Wild and %Male represent percentages of wild-born fish and of males in each run year, respectively.

In Su94–97 and Wi91, traditional hatchery programs were operated individually for summer run and winter run, and all the returned fish were allowed to pass above the dam. In Su98 and Wi92–94, almost none of the returned fish born in the traditional hatcheries were allowed to pass above the dam, so that only wild-born fish could reproduce in these run years. In Wi95–98, both wild-born fish and fish from a supplementation hatchery had returned to the river, and the numbers of hatchery-born fish passed above the dam were controlled to be < 50% of all the fish allowed to pass.

numbers of individuals used in this study were 4561 for summer-run parents, 2217 for summer-run offspring, 3945 for winter-run parents, and 5991 for winter-run offspring. Note that the parental samples include both wild-born and hatchery-born fish, whereas the offspring samples include only wild-born fish (Table 2).

#### Hatchery programs in the Hood River

Traditional hatchery stocks,  $H_{\text{trad}}$ , are produced using nonlocal brood stock that has spent multiple generations in hatcheries. Supplementation hatchery stocks,  $H_{\text{supp}}$ , are produced using local, wild fish as broodstock. The Hood River has been stocked by the ODFW since 1960s with winter-run and summer-run  $H_{\text{trad}}$ . The winter-run  $H_{\text{trad}}$  was phased out of the Hood River in the early 1990s, while the summer-run  $H_{\text{trad}}$  was phased out in the late 1990s. The supplementation programme of steelhead in this river started in 1991 for the winter-run populations, and in 1997 for the summer-run populations. The winter-run  $H_{\text{supp}}$  began breeding in the river in appreciable numbers in 1995, and the summer-run  $H_{\text{supp}}$  in 2001. Details of the supplementation

program are described in Olsen (2003) and Araki *et al.* (2006).

In Su94–97 and Wi91, all the returning fish were allowed to pass above the dam, including high proportions of  $H_{\text{trad}}$  (Table 2). As part of an effort to phase out  $H_{\text{trad}}$ , almost none of the traditional hatchery-born fish were allowed to pass above the dam in Su98 and Wi92–94. Thus, almost all of the winter-run fish that reproduced in run years Wi92–94 were wild-born. In Wi95–98, appreciable numbers of  $H_{\text{supp}}$  started to return, and the number of  $H_{\text{supp}}$  passed above the dam was controlled to be < 50% of all the fish allowed to pass, to avoid a predominance of hatchery-born spawners in this river (and hence in the gene pool of the populations).

#### Microsatellite loci and parentage analysis

Genotypes at eight microsatellite loci (Omy1001, Omy1011, Omy1191, Omy77, One108, One2, Ssa407, and Str2, see Araki *et al.* 2006 for details) were identified for these samples. We followed a standard Chelex protocol for DNA extraction and amplification (see Nelson *et al.* 1998), with

minor modifications (50–55 °C of annealing temperature). The genotype scoring was done on an ABI 3100 capillary electrophoresis system (Applied Biosystems, California). We successfully genotyped 97.6% of the fish that returned to the river as adults (Table 2), at up to eight loci. The average number of genotype-determined loci was 7.77 per sample. Part of the genotype data was used in Araki *et al.* (2006).

We used an exclusion method to make parentage assignments (Araki *et al.* 2006). Putative parent-offspring pairs sharing at least six loci (some fish had missing data) and having no mismatching loci were assigned to parent-offspring pairs using the CERVUS program (Marshall *et al.* 1998). In the few cases that more than one candidate parent shared no mismatch to an offspring, the parent with the highest LOD score was assigned. Total exclusionary powers were at least 0.9996 in all cases.

### Estimating the whole (census) population size

To estimate the ratio  $N_e/N$ , the census population size was estimated based on the run size (census size of returned anadromous adults,  $N_{\text{anad}}$ ). Because our samples were collected at the complete upstream barrier to steelhead, parental population size listed in Table 2 represents virtually all the anadromous fish potentially reaching the spawning grounds. As mentioned above, however, noticeable numbers of parents turned out to be missing from the dataset in the parentage assignment (Araki *et al.* 2006), suggesting that nonanadromous parents produced a substantial number of anadromous offspring.

To take the nonanadromous parents into consideration for estimating parental  $N$  ( $\hat{N}$ ), we calculated  $\hat{N}$  for each sex separately as follows:

$$\hat{N} = \frac{N_{\text{anad}}}{\hat{P}_{\text{sampled}}} \quad (\text{eqn 1})$$

$$\hat{P}_{\text{sampled}} = \frac{1}{(1-\hat{a})(1-\hat{b})} \left( \frac{N_{\text{assigned}}}{N_{\text{offspring}}} - \hat{b} \right) \quad (\text{eqn 2})$$

where  $\hat{P}_{\text{sampled}}$  is the proportion of offspring whose parent is in the sample (either father or mother),  $N_{\text{offspring}}$  and  $N_{\text{assigned}}$  are numbers of returned offspring and assigned offspring, and  $\hat{a}$  and  $\hat{b}$  are the type-A and type-B error rates, respectively (Araki & Blouin 2005; Araki *et al.* 2006). The type-A error rate is the rate for failing to assign a true parent when that parent is in the sample, and the type-B error rate is the rate at which nonparents are incorrectly assigned to offspring. In this study, we used the error rates previously estimated based on the same dataset and the same criteria of parentage assignment  $\hat{a} = 15.6\%$  and  $\hat{b} = 1.75\%$  for male parents and  $\hat{a} = 5.7\%$  and  $\hat{b} = 1.97\%$  for female parents, which were estimated using known parent-offspring pairs of brood stock and their hatchery-born offspring from run years Wi93 and Wi94 in Araki *et al.*

(2006)]. After obtaining  $\hat{N}$  for each sex,  $\hat{N}$  for each run year was calculated as:

$$\hat{N}_{[\text{run-year}]} = \hat{N}_{[\text{male}]} + \hat{N}_{[\text{female}]}$$

to estimate  $\hat{N}_b/\hat{N}$ . For  $\hat{N}_e/\hat{N}$ ,  $\hat{N}$  in each generation was calculated simply by summing up  $\hat{N}_{[\text{run-year}]}$  within each generation.

An important assumption here is that the ratio of the numbers of nonsampled 'parents' to sampled 'parents' is the same as the ratio of the numbers of 'offspring' whose parents were not sampled to those sampled (i.e.  $[1 - P_{\text{sampled}}]/P_{\text{sampled}}$ ). This assumption holds only when the mean reproductive success ( $\bar{k}$ ) among nonsampled parents is equal to  $\bar{k}$  among sampled parents, and may be unrealistic considering differences in phenotypes and reproductive strategies between anadromous and nonanadromous fish. To confirm the robustness of our conclusions against a violation of this assumption, a simple assumption of equal numbers of sampled and nonsampled parents ( $\hat{N} = 2N_{\text{anad}}$ ) was also made and the results were compared.

Angling for hatchery steelhead trout was allowed above the dam in a limited area during 1993–98. We used the ODFW upper-bound estimates of the harvest rate on hatchery fish in the Hood River of 25% for Su94–97, 5.0% for Wi95, 20% for Wi96–97 (E. Olsen, personal communication) to estimate the minimum number of potential spawners in those years.

### Demographic estimate of $N_e$

Based on the parentage assignments, the mean ( $\bar{k}$ ) and variance ( $V_k$ ) of reproductive success among parents were estimated for each sex in each parental population. Because parentage assignment errors can affect the estimation of  $\bar{k}$  and  $V_k$ , we first adjusted the observed  $\bar{k}$  using the method of Araki & Blouin (2005). An unbiased estimate of  $\bar{k}$  ( $\bar{k}_{[\text{obs}]}$ ) was obtained by correcting the bias caused by the assignment errors ( $a$  and  $b$  above) using equation 13 in Araki & Blouin (2005). Because we could not directly estimate an unbiased  $V_k$ , we adjusted the observed index of variability ( $V_{k[\text{obs}]}/\bar{k}_{[\text{obs}]}$ ) to obtain an adjusted value by:

$$\left[ \frac{V_{k[\text{adj}]}}{\bar{k}_{[\text{adj}]}} \right] \approx 1 + \frac{\bar{k}_{[\text{adj}]}}{\bar{k}_{[\text{obs}]}} \left( \frac{V_{k[\text{obs}]}}{\bar{k}_{[\text{obs}]}} - 1 \right) \quad (\text{eqn 3})$$

where  $V_{k[\text{adj}]}$  is the adjusted variance in reproductive success (Crow & Morton 1955; Waples 2002b). While this approximation was originally applied to adjust the index of variability between different life stages (equation 14 in Crow & Morton 1955), we applied it to adjust the index for  $\bar{k}_{[\text{adj}]}$  (unbiased estimate of  $\bar{k}$ ) here.

After adjusting  $V_k/\bar{k}$  for the assignment bias, we estimated the inbreeding  $N_b$  for each sex ( $N_{b[\text{female}]}$  or  $N_{b[\text{male}]}$ ) using:

$$N_b \approx \frac{\bar{k}N - 2}{\bar{k} - 1 + V_k/\bar{k}} \quad (\text{eqn 4})$$

(Crow & Kimura 1970; Caballero 1994), and the estimate of  $N_b$  in run year  $i$  ( $N_{b[i]}$ ) was obtained using:

$$N_{b[i]} = \frac{4(N_{b[\text{female}]} \times N_{b[\text{male}]})}{(N_{b[\text{female}]} + N_{b[\text{male}]})} \quad (\text{eqn 5})$$

Finally,  $N_e$  for one generation was estimated using:

$$N_e = \frac{1}{\sum (X_i^2/N_{b[i]})} \quad (\text{eqn 6})$$

where  $X_i$  is the proportional contribution of breeders in run year  $i$  to the next generation (Waples 2002a, 2006a). For simplicity, five years/generation for summer run and four years/generation for winter run were assumed (see above). Using the samples from five summer-run years and eight winter-run years, we therefore obtained  $N_e$  in one complete generation of summer run and in two complete generations of winter run in this study.

For general comparisons of the index of variability, equation 3 was further used for scaling to  $\bar{k} = 2$  (by replacing  $\bar{k}_{[\text{adj}]}$  with 2). We call it the scaled index of variability, contrasting to the adjusted index of variability above (Table 1). Note that inbreeding  $N_b$  based on the adjusted index of variability is almost identical to variance  $N_b$  based on the scaled index of variability (Waples 2002b).

### Evaluating reduction factors of $N_e$

To examine the importance of sex ratio and two components of variance in reproductive success (variance among individuals within years and variance in  $\bar{k}$  across years within a generation) on reducing  $N_e/N$ , we calculated  $N_e/N$  independently for each of these factors.

To evaluate the effect of sex ratio, we first calculated the proportion of male parents ( $P_{\text{male}}$ ) by adding up all the numbers of males and females in a generation (Table 2). Equation 5 provides an estimate of  $N_e/N$  reflecting only the sex ratio as  $4P_{\text{male}}(1 - P_{\text{male}})$ . The reduction rate was then calculated as  $(1 - N_e/N)$ . In this case,  $N_e/N = 1$  (reduction rate = 0) when the sex ratio is 1 : 1.

Likewise, equation 4 can provide an estimate of  $N_e/N$  affected only by the variance in reproductive success among individuals. To evaluate this effect, we first calculated an overall  $V_k/\bar{k}$  as the geometric mean (GM) of the scaled  $V_k/\bar{k}$  ( $\bar{k} = 2$ ) over run year and sex, ignoring the sex ratio bias and the difference in  $N$  among run years. Equation 4 was then used for estimating  $N_e$  (instead of  $N_b$  in equation 4), by replacing  $N$  in each run year with  $\hat{N}_{\text{total}}$  (total  $\hat{N}$  in a generation, Table 3). The reduction rate by this factor is given as:

$$(1 - \hat{N}_e/\hat{N}_{\text{total}})$$

Here we ignore prespawning mortalities, which are estimated as 10% for summer run and 5% for winter run (E. Olsen, personal communication), because this factor affects the expectations of  $N_e/N$  only slightly, as is apparent from equation 4. In this case,  $N_e = (N - 1)$  when the scaled  $V_k/\bar{k} = 1$ .

Finally, we evaluated the effect of variance in  $\bar{k}$  across years within a generation (see Waples 2006a). Equation 6 can provide an estimate of  $N_e$  reflecting only this factor, by replacing  $N_{b[i]}$  with  $\hat{N}$  in each run year (Table 3). Again, the reduction rate was given as  $(1 - \hat{N}_e/\hat{N}_{\text{total}})$ , but in this case  $N_e/N = 1$  when  $\bar{k}$  is constant among run years within a generation ( $\bar{k} = \text{total number of offspring in a generation divided by } \hat{N}_{\text{total}}$  in this case).

### Distribution of family size

For some example years, we compared the observed distribution of family size with that expected under the Poisson and negative binomial distributions. The Poisson distribution characterizes an ideal population with  $N_b = N$ . The negative binomial distribution represents an overdispersed Poisson distribution with  $V_k > \bar{k}$  and  $N_b < N$ . We used a two-step process to generate a negative binomial distribution with the same mean and variance in family size as the observed distribution (Anderson 2001; Waples 2006b). First, a random sample was taken from a gamma distribution with the appropriate shape and scale parameters. Next, this gamma random number was used as the parameter for a Poisson distribution, from which a random number was drawn to represent the family size of one individual. This process was repeated 200 000 times to generate a smooth, negative binomial distribution of expected family size. Goodness of fit to the observed distribution was evaluated by a chi-square test with 27 classes (family sizes ( $k$ ) = 0–25, and a combined class for  $k > 25$ ) and 24 degrees of freedom.

This two-stage process departs from the standard Wright-Fisher ideal population in having both a random and a directed process (Anderson 2001). In an ideal population, each individual contributes equally to an infinite gamete pool, from which the next generation is randomly drawn. In the two-step model, the  $i$ th individual contributes  $G_i$  gene copies to the gamete pool, with  $G_i$  following the gamma distribution. When the next generation is randomly drawn from this gamete pool, the result is a larger variance in family size than occurs in an ideal population.

## Results

### Variance in reproductive success

Estimated indexes of variability ( $V_k/\bar{k}$ ) are shown for each sex in Table 3. The  $V_k/\bar{k}$  scaled to  $\bar{k} = 2$  was 5.8–17.3 for

**Table 3** Demographic estimate of  $N_b$ ,  $N_e$ , and  $N_e/N$ 

Run year	$\hat{N}$	Adjusted $V_k/\bar{k}$		Scaled $V_k/\bar{k}$ ( $\bar{k}=2$ )		$\hat{N}_b$	$\hat{N}_b/\hat{N}$	$\hat{N}_b/2N_{\text{anad}}$
		Male	Female	Male	Female			
Summer run (Su)								
Su94	2506	1.5	1.4	8.4	7.6	547.4	0.22	0.15
Su95	1518	1.2	2.7	10.3	17.3	204.2	0.13	0.16
Su96	1902	2.7	2.2	6.7	6.7	478.3	0.25	0.16
Su97	1500	3.6	3.0	9.4	9.7	278.4	0.19	0.26
Su98	927	1.0	2.3	6.0	5.8	230.6	0.25	0.85
Su total	8354	2.0*	2.3*	8.0*	8.7*	1425.9**	0.17	0.15
Winter run generation 1 (Wi-1)								
Wi91	1781	2.0	1.7	7.7	4.9	491.6	0.28	0.24
Wi92	710	3.5	2.1	6.5	3.6	228.6	0.32	0.28
Wi93	760	2.2	1.6	4.4	3.0	314.3	0.41	0.41
Wi94	512	2.3	2.4	3.9	2.4	233.8	0.46	0.56
Wi-1 total	3762	2.4*	1.9*	5.4*	3.3*	1095.5**	0.29	0.27
Winter run generation 2 (Wi-2)								
Wi95	700	6.5	4.7	4.2	2.7	316.7	0.45	0.34
Wi96	921	3.5	2.1	3.3	2.1	501.1	0.54	0.44
Wi97	868	2.8	2.9	3.0	2.6	452.1	0.52	0.54
Wi98	1395	2.8	1.9	5.2	3.0	541.8	0.39	0.52
Wi-2 total	3884	3.6*	2.7*	3.8*	2.6*	1505.3**	0.40	0.38

$\hat{N}$  represents an estimate of census population size in a parental population, based on equation 1.  $V_k/\bar{k}$  is the index of variability, estimated based on the parentage analysis. Adjusted  $V_k/\bar{k}$  was estimated only by adjusting parentage assignment errors, whereas scaled  $V_k/\bar{k}$  was weighted by  $\bar{k}=2$  (see Table 1 for precise definitions).  $\hat{N}_b$  was estimated by the demographic method using equation 5.

\*Geometric mean among run years within a generation.

\*\* $N_e$  per generation estimated based on equation 6.

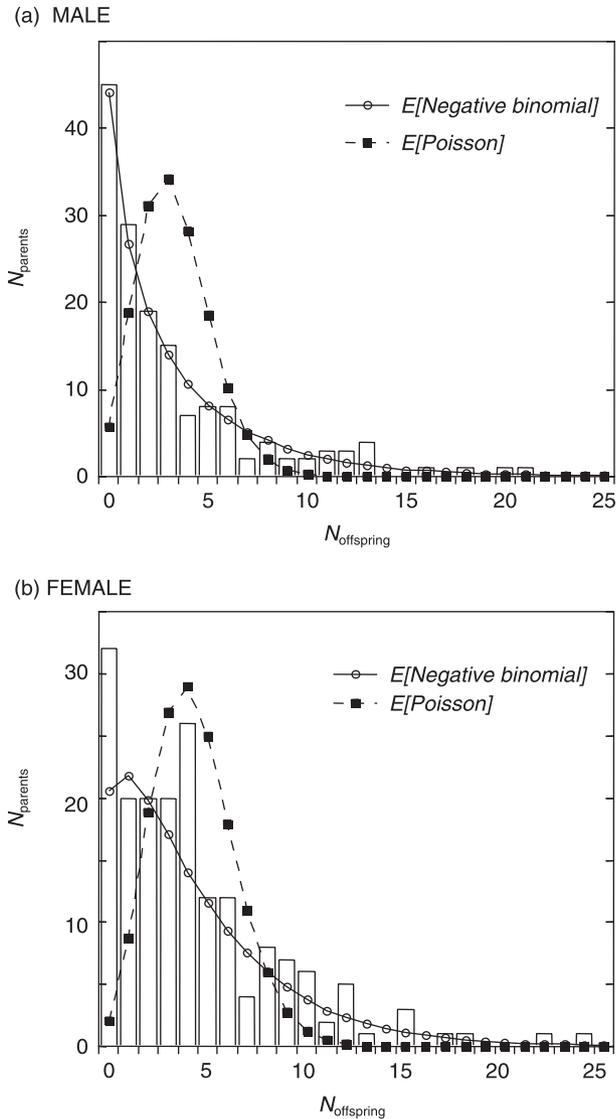
summer run (GM = 8.0 for male, 8.7 for female) and 2.1–7.7 for winter run (GM = 4.5 for male, 2.9 for female), suggesting larger variance in reproductive success in both sexes and both populations compared with that expected for a Poisson distribution ( $V_k/\bar{k}=1$ ). Indeed, some individuals evidently left > 20 offspring that returned to the river successfully, despite little or no reproductive success for most parents (Fig. 1 for example of Wi95). Males had significantly higher scaled  $V_k/\bar{k}$  than females in all run years of winter run ( $F$ -test after square-root transformation,  $P=0.000$ – $0.035$ , combined  $P<0.001$ ), whereas the difference between sex was not significant in summer run except Su91 ( $P=0.002$ – $1.0$ , combined  $P=0.039$ ).

The example shown in Fig. 1 illustrates the dramatic difference between the observed distribution of family size and that expected from a Poisson distribution. In contrast, the fit to the negative binomial distribution was very good for the males (chi square = 19.7; d.f. = 24;  $P>0.5$ ) and not quite as good for the females (chi square = 44.0; d.f. = 24;  $0.005 < P < 0.01$ ) but still dramatically better than the fit to the Poisson distribution. This result suggests that reproductive success in *Oncorhynchus mykiss* can be modelled as a two-stage process resulting in an overdispersed Poisson distribution, at least in some cases. The explanation for the

slightly poorer fit for the female example (Fig. 1b) is not clear, but factors that might be involved include a high rate of infertility and/or inaccurate estimates of harvest mortality (both of which could inflate the number of families leaving no offspring) and chance events.

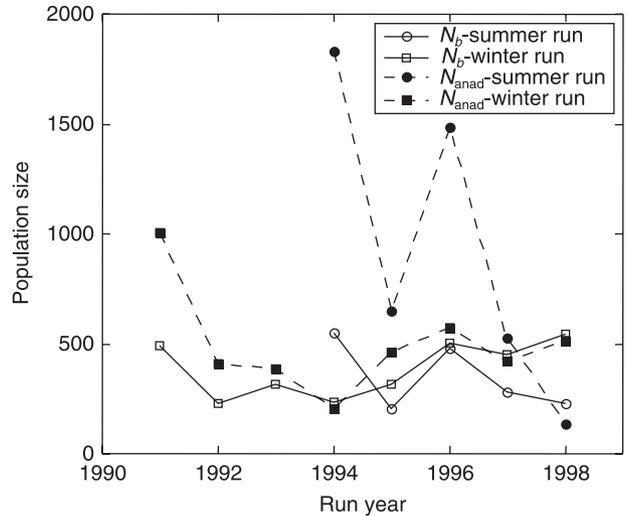
#### Demographic estimate of effective population size

Estimated  $N_b$  was very similar in the two run populations (204–547 in summer run and 229–542 in winter run, Table 3). These estimates were also relatively stable among run years, despite the highly variable census size of anadromous adults ( $N_{\text{anad}}$ ) in these run years (Fig. 2). The unbiased estimates of coefficient of variation (CV, Sokal & Rohlf 1995) in  $\hat{N}_b$  were lower than in  $N_{\text{anad}}$  in both populations (CV[ $\hat{N}_b$ ] = 46.8 < CV[ $N_{\text{anad}}$ ] = 80.0 in summer run, CV[ $\hat{N}_b$ ] = 33.7 < CV[ $N_{\text{anad}}$ ] = 48.1 in winter run), indicating stable  $\hat{N}_b$  relative to  $N_{\text{anad}}$ .  $\hat{N}_e$  (per generation) was 1096–1505, and overall  $\hat{N}_e/\hat{N}$  ratio was 0.17–0.40 (Table 3). These ratios were very similar to  $\hat{N}_e/(2N_{\text{anad}})$ , suggesting that the results were not biased by errors in estimating the census population sizes. One exception among run year was  $\hat{N}_b/(2N_{\text{anad}}) = 0.85$  in Su98, which was clearly different from  $\hat{N}_b/\hat{N}$  in the same run year ( $\hat{N}_b/\hat{N} = 0.25$ , see below).



**Fig. 1** Example histograms for number of offspring produced by each parent in Wi95. Male (a) and female (b), and observed number from parentage assignments (open bar), expected number from a negative binomial (open circle), and expected number from Poisson distribution (closed square) were drawn separately (see Materials and methods).  $\bar{k}_{[obs]}$  was 3.3 for male and 4.4 for female, and  $V_{k[obs]}$  was 18.1 for male and 18.4 for female in Wi95. Among male, for example, 45 males left no returning offspring, whereas one male left 21 offspring in Wi95. Note that the observed numbers are considered as minimum estimates, because assignment-error biased these estimates downward and because we used the ODFW upper-bound estimates of the harvest rate.

Given the observed sex ratio in anadromous parents (Table 2), census sizes of anadromous adults in each run year, and the estimated (scaled) index of variability (Table 3), we evaluated how much reduction of  $N_e$ , relative to  $N$ , was caused by these factors (Table 4). The reduction rates  $(1 - N_e/N)$  were estimated as only 2.3%–5.4% by une-



Summer run |  $H_{trad}$  and  $W$  |  $W$  only  
 Winter run  $H_{trad}$  and  $W$  |  $W$  only |  $H_{supp}$  and  $W$

**Fig. 2** Estimated effective number of breeders ( $N_b$ ) and run sizes ( $N_{anad}$ ) in two populations of steelhead in the Hood River. The summer run population is shown by circles (open circle for  $N_b$ , closed circle for  $N_{anad}$ ) and the winter run population is shown by squares (open for  $N_b$ , closed for  $N_{anad}$ ).  $H_{trad}$  and  $W$ : run year with a high proportion of traditional hatchery-born fish,  $W$  only: run year with virtually wild fish only, and  $H_{supp}$  and  $W$ : run year with up to 50% of supplementation hatchery-born fish. The unbiased estimates of coefficient of variation (Sokal & Rohlf 1995) were 80.0 for  $N_{anad}$  and 46.8 for  $\hat{N}_b$  in summer run, 48.1 for  $N_{anad}$  and 33.7 for  $\hat{N}_b$  in winter run, representing stable  $\hat{N}_b$  relative to  $N_{anad}$ .

**Table 4** Effects of sex ratio and variance in reproductive success on  $N_e/N$

Generation	Su	Wi-1	Wi-2
Reduction rate by each factor (%)			
unequal sex ratio	5.4	2.3	2.7
variance in reproductive success			
variance in $\bar{k}$ among run years	19.9	22.4	19.2
large $V_k/\bar{k}$ among individuals	78.5	61.9	51.7
Total expected $N_e/N$	0.16	0.29	0.38
Observed $\hat{N}_b/\hat{N}^*$	0.17	0.29	0.40

Total expected  $N_e/N$  was calculated by multiplying [1 – reduction rate] for the three reduction factors within each generation.

\*Data from Table 3.

qual sex ratio, but variance in reproductive success had a huge impact on  $N_e$  (reduction rate = 52%–79% by variance in reproductive success among individuals and 19%–22% by variance in  $\bar{k}$  across years within a generation), suggesting that high variance in reproductive success is a primary cause of  $\hat{N}_e/\hat{N} < 1$  in these populations.

Assuming an independence of these factors, we obtained an expected  $N_e/N$  that was very similar to the  $\hat{N}_e/\hat{N}$  (Table 4), suggesting that the assumption of independence was reasonable. However, it is noteworthy that these estimates are based on the information only from anadromous parents. The parental population as a whole (including nonanadromous fish) may have different reduction rates and hence different  $N_e/N$ .

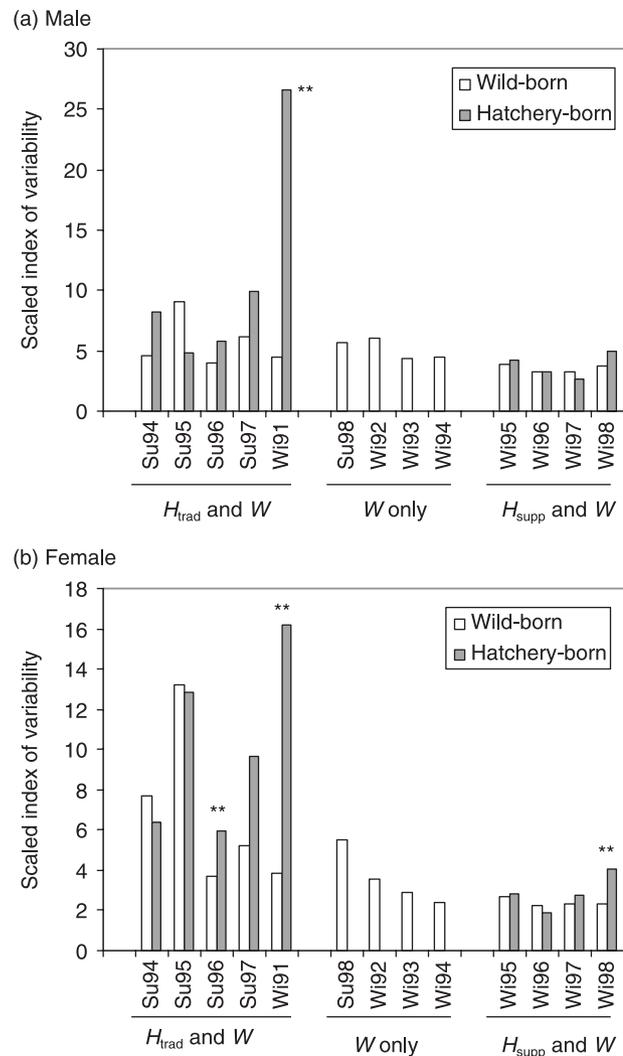
#### Effects of hatchery-born fish on $N_b$

Notably poor reproductive success is evident in the  $H_{\text{trad}}$  (Araki *et al.* 2006), which is the primary reason for the poor recruitment in Su94–97 and Wi91 ( $N_{\text{Offspring}}/N_{\text{anad}}$ , Table 2). Comparing with scaled  $V_k/\bar{k}$  in run years with mostly wild-born fish (Su98, Wi92–94), the larger scaled  $V_k/\bar{k}$  in Su94–97 and Wi91 (Table 3) indicates that the poor performance of  $H_{\text{trad}}$  led to high variance in reproductive success in the natural spawners as a whole (which is a primary factor causing small  $N_e/N$ ). Separate estimates of the scaled  $V_k/\bar{k}$  for the wild-born parents and for the hatchery-born parents in the same run years support this view (Fig. 3). The scaled  $V_k/\bar{k}$  varied substantially between the wild-born and  $H_{\text{trad}}$  parents (e.g. in Su94 scaled  $V_k/\bar{k}$  was 4.2 in wild-born males and 8.2 in  $H_{\text{trad}}$  males). The geometric mean of the scaled  $V_k/\bar{k}$  in Su94–97 was 5.7 in wild-born male, 6.9 in  $H_{\text{trad}}$  male, 6.7 in wild-born female, and 8.3 in  $H_{\text{trad}}$  female. Interestingly however, the scaled  $V_k/\bar{k}$  were not always higher in  $H_{\text{trad}}$  parents than in wild-born parents in some run years. In Su95, for example, wild-born parents had exceptionally high  $V_k/\bar{k}$  in both sexes (Fig. 3). The reason why the scaled  $V_k/\bar{k}$  in wild-born parents in Su94–97 are more variable than in the other run years is unclear (see Discussion).

The scaled  $V_k/\bar{k}$  in  $H_{\text{supp}}$  parents, on the other hand, were close to those in the wild-born parents and to their overall  $V_k/\bar{k}$  in run years Wi95–98 (except Wi98 female, Fig. 3). The geometric mean of the scaled  $V_k/\bar{k}$  was 3.5 in wild-born male, 3.7 in  $H_{\text{supp}}$  male, 2.4 in wild-born female, and 2.8 in  $H_{\text{supp}}$  female in Wi95–98. The scaled  $V_k/\bar{k}$  in Wi95–98 (with  $H_{\text{supp}}$ ) were also similar to those in Wi92–94 (almost no hatchery fish returned), suggesting little effect by  $H_{\text{supp}}$  on the index of variability in the natural spawners.

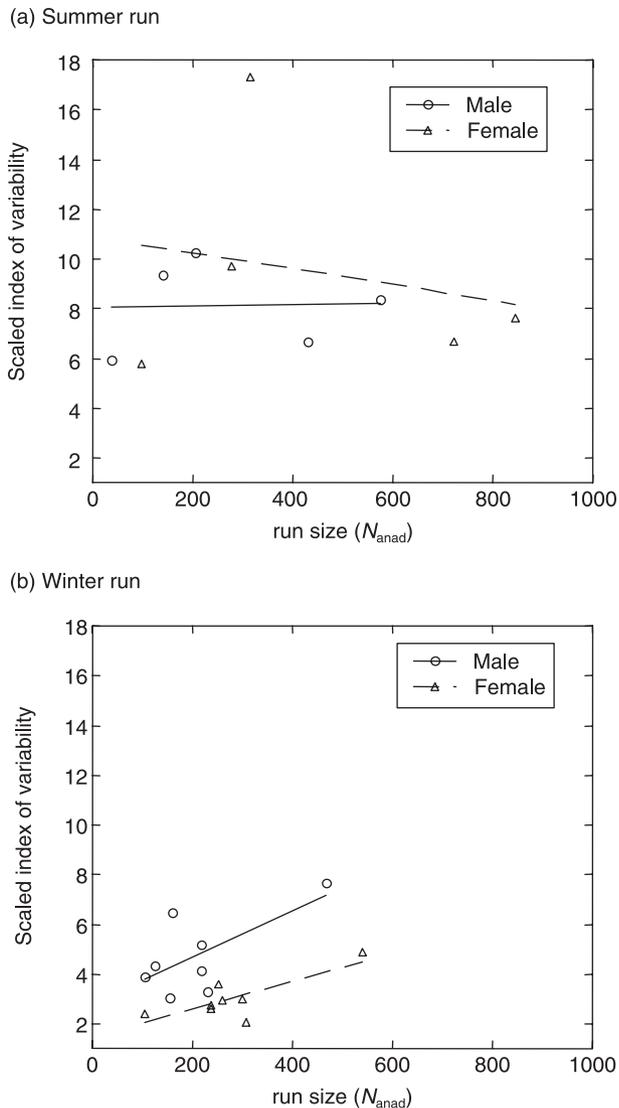
#### Genetic compensation

The stable  $N_b$  among run years relative to highly variable run sizes of anadromous adults (Fig. 2) indicates that some kind of compensation may have occurred. Indeed, Ardren & Kapuscinski (2003) found a density-dependent  $N_b/N$  in a steelhead population, suggesting 'genetic compensation' in which reduction in  $N_b$  is buffered when  $N$  is small, presumably owing to reduction in competition for mates or spawning sites ('genetic compensation *within anadromous*



**Fig. 3** The scaled index of variability (the scaled  $V_k/\bar{k}$ ) among wild-born parents (white bar) and hatchery-born parents (dark bar) in run years.  $H_{\text{trad}}$  and W: run year with a high proportion of traditional hatchery-born fish, W only: run year with virtually wild fish only, and  $H_{\text{supp}}$  and W: run year with up to 50% of supplementation hatchery-born fish. Difference in the scaled  $V_k/\bar{k}$  between hatchery and wild fish was tested using  $F$ -test, after square-root transformation to adjust the skewed distribution of the number of offspring per parent (\*\* $P < 0.01$ ). Comparing results among different run years, disturbance in the index of variability ( $V_k/\bar{k}$ ) by traditional hatchery-born parents is evident, suggesting a negative effect of traditional hatchery programmes on the index of variability (and hence on  $N_b/N$ ). No such effect by the supplementation hatchery-born fish is detected, although  $H_{\text{supp}}$  females have significantly large  $V_k/\bar{k}$  relative to wild females that returned in the same year in Wi98 ( $P < 0.001$ ).

*steelhead population'*, hereafter). In this case, positive correlation between  $V_k/\bar{k}$  and anadromous run size is expected. However, we found no evidence for such a correlation between scaled  $V_k/\bar{k}$  and  $N_{\text{anad}}$  in the summer-run population ( $r = 0.03$ ,  $P = 0.962$  for male,  $r = -0.22$ ,  $P = 0.727$



**Fig. 4** Relationship between variance in reproductive success and run size among run years. Summer run (a) and winter run (b), and male (solid line and circle) and female (dotted line and triangle).  $V_k/\bar{k}$  was scaled to  $\bar{k}=2$  (see Materials and methods).  $r=0.03$ ,  $P=0.962$  for summer-run male,  $r=-0.22$ ,  $P=0.727$  for summer-run female,  $r=0.70$ ,  $P=0.051$  for winter-run male, and  $r=0.78$ ,  $P=0.024$  for winter-run female by two-tailed  $t$ -test. The marginal significances for the winter run become nonsignificant, however, if the Wi91 data (the rightmost points for both sexes in B) are removed ( $r=0.09$ ,  $P=0.84$  for male,  $r=0.15$ ,  $P=0.75$  for female. See Discussion).

for female by two-tailed  $t$ -test, Fig. 4a). The correlation between scaled  $V_k/\bar{k}$  and  $N_{\text{anad}}$  was positive and moderately significant in the winter-run population ( $r=0.70$ ,  $P=0.051$  for male, and  $r=0.78$ ,  $P=0.024$  for female, Fig. 4b), but was not significant if the Wi91 data are removed (the rightmost points for both sexes in Fig. 4b). In Wi91,  $V_k/\bar{k}$  was substantially increased by traditional hatchery-born

parents (Fig. 3). Overall therefore we found no evidence for compensation within anadromous steelhead population in the summer run and at best weak evidence for the winter run.

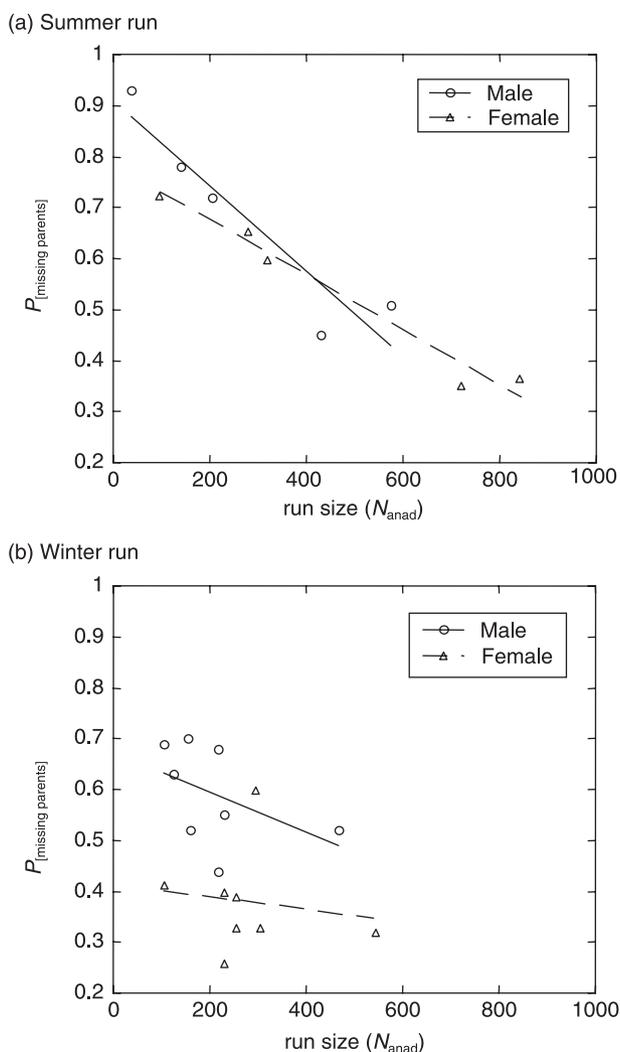
Another possible explanation for the stable  $N_b$  is 'genetic compensation between life-history forms'. As we mentioned above, the interbreeding between life-history forms (anadromous and nonanadromous fish, in this case) might stabilize  $N_b$  among run years in the face of fluctuating census sizes. Because we obtained almost complete samples from anadromous parents, offspring whose parents were missing from our data must be attributed to the reproductive contribution of nonanadromous parents. Note that the missing parents are not an artefact caused by parentage assignment errors, because we took assignment errors into consideration (see Materials and methods). We found negative correlations between  $N_{\text{anad}}$  and the proportion of offspring with one or both parents missing in both runs and both sexes (Fig. 5), and the result from the summer run population was statistically significant ( $r=-0.93$ ,  $P=0.021$  for male,  $r=-0.98$ ,  $P=0.004$  for female in summer run, and  $r=-0.45$ ,  $P=0.27$  for male,  $r=-0.14$ ,  $P=0.75$  for female in winter run). Overall, the combined probability of both sexes in the two populations (Sokal & Rohlf 1995) was also statistically significant ( $P=0.004$ ). This relationship also explains why  $\hat{N}_b/2N_{\text{anad}}$  was so different from  $\hat{N}_b/\hat{N}$  in Su98 (Table 3), because in this run year  $N_{\text{anad}}$  was the smallest and  $\hat{N}$  was  $5.8 N_{\text{anad}}$  rather than  $2N_{\text{anad}}$ .

## Discussion

The principle results that emerged from our analyses are as follows: (i) the steelhead populations in the Hood River showed a large variance in reproductive success, which is the primary cause of the reduction in  $N_e/N$ ; (ii) the traditional hatchery-born fish had negative effects on  $N_b$ , not only by decreasing the mean reproductive success of the natural population but also by increasing the variance in reproductive success; and (iii) both run populations showed relatively stable  $N_b$  among run years and a negative correlation between anadromous run size and inferred reproductive contribution of nonanadromous parents. These results suggest a genetic compensation between life-history forms in this species. These points and their general implications are discussed below.

### Variance in reproductive success in salmonids

The geometric means of the scaled  $V_k/\bar{k}$  were 8.0 in summer-run males, 8.7 in summer-run females, 4.5 in winter-run males, and 2.9 in winter-run females (Table 3). Although the large  $V_k/\bar{k}$  in summer-run will be in part due to the influence of traditional hatchery fish (Fig. 3), the scaled  $V_k/\bar{k}$  was also large in Su98 (5.77–5.95), in which almost no hatchery fish returned. The only comparable



**Fig. 5** Negative correlation between the proportion of offspring with at least one parent missing from the data ( $P_{\text{[missing parents]}}$ ) and run size among run years.  $P_{\text{[missing parents]}}$  was estimated for each sex using equation 2 and  $P_{\text{[missing parents]}} = (1 - P_{\text{sampled}})$ . Summer run (a) and winter run (b), and male (solid line and circle) and female (dotted line and triangle).  $r = -0.93$ ,  $P = 0.021$  for summer-run male,  $r = -0.98$ ,  $P = 0.004$  for summer-run female,  $r = -0.45$ ,  $P = 0.267$  for winter-run male, and  $r = -0.14$ ,  $P = 0.747$  for winter-run female by two-tailed  $t$ -test. Overall, the combined probability for the negative correlation was 0.004.

published data from a natural salmonid population are for Atlantic salmon (*Salmo salar* L. Garant *et al.* 2001), in which unscaled  $V_k/\bar{k}$  for juvenile samples was 8.6 for males and 8.9 for females. After scaling the *Salmo* data to  $\bar{k} = 2$ , however, the index of variability dropped to 2.05 for males and 1.94 for females – much lower than we found for the steelhead populations. Results for some experimental hatchery populations of Pacific salmon also show less variance in reproductive success than we report here (scaled  $V_k/\bar{k} = 1.1\text{--}5.1$ ; see Waples 2004 for reviews). Although

further studies are necessary before general conclusions are drawn, this result indicates that steelhead populations in the Hood River have unusually large variance in reproductive success among individuals, even within salmonids. It is also noteworthy that males had significantly higher scaled  $V_k/\bar{k}$  than females in winter-run population, as observed in other salmonids (Garant *et al.* 2003).

#### *Effects of different types of artificial propagation on $N_e$*

Given the poor reproductive success of  $H_{\text{trad}}$  (Araki *et al.* 2006), the negative effect on  $N_b$  may not be surprising. However, in Su94–97 and Wi91, in which  $H_{\text{trad}}$  dominated, the variance in reproductive success of hatchery-born parents was high. Given that variance in reproductive success is the primary cause of  $N_e/N < 1$ , this result clearly suggests that  $H_{\text{trad}}$  decreased the effective size of the natural populations. Furthermore, the variance in reproductive success of wild-born fish was also increased in some of these run years. The cause of this increase is unclear, but one possible explanation is an indirect effect of  $H_{\text{trad}}$  on the natural populations. Under this scenario, variance in reproductive success is increased not only because of poor reproduction by the  $H_{\text{trad}}$  parents, but also by reduced reproductive success of wild-born parents that mated with the  $H_{\text{trad}}$  parents. Indeed, such a negative interaction was indicated between wild-born and  $H_{\text{trad}}$  parents (but not between wild-born and  $H_{\text{supp}}$  parents, Araki *et al.* 2006). If this is the case, the presence of  $H_{\text{trad}}$  has a direct impact on  $N_e$  in the natural population, and the removal of  $H_{\text{trad}}$  fish should increase  $N_e$  in subsequent generations, as expected in some situations (Ryman & Laikre 1991).

Similarities between wild-born and  $H_{\text{supp}}$  parents in reproductive success (Fig. 3, see also Araki *et al.* 2006) indicate that supplementation hatchery-born fish may actually support the natural populations.  $\hat{N}_e$  in the winter run generation-2 (Wi95–98) was 37% larger than generation-1 (Wi91–94, Table 2), and  $N_b$  was gradually increasing in winter run during 1995–98 (Fig. 2). These favourable results for conservation purposes in the winter run population might or might not be caused by the supplementation program, but we certainly found no sign of a negative effect of the program on the effective size of the natural population.

One caveat is that all the  $\hat{N}_e$  in this study were estimated based on direct information only from the anadromous offspring, and do not include nonanadromous offspring. Given that the frequent reproductive interaction in *Oncorhynchus mykiss*, production of nonanadromous offspring by anadromous parents is also likely to occur. If so, overall  $\hat{N}_e$  (including both anadromous and nonanadromous offspring) can be different when different types of parents (wild-born,  $H_{\text{trad}}$  and  $H_{\text{supp}}$ ) reproduce anadromous and nonanadromous offspring differently, as suggested in brown trout (*Salmo trutta* L., Hansen *et al.* 2000).

*N<sub>e</sub>/N ratio*

The estimated  $\hat{N}_e/\hat{N}$  in this study (0.2–0.4) were not only between the ranges of estimates reported in this species in previous studies (0.1–0.3, Heath *et al.* 2002; 0.5–0.7, Ardren & Kapuscinski 2003), but also within the range of  $N_e/N$  that is suggested both theoretically and empirically for the single-generation  $N_e/N$  in various mating systems (0.3–0.5; see Nunney 1993, 1995; Frankham 1995b; Waples 2004 for reviews). The dominant effect of variance in reproductive success on reducing  $N_e/N$  was also consistent with the other studies on salmonids (Ardren & Kapuscinski 2003; Hedrick 2005b), suggesting that variance in reproductive success truly is the key factor to reduce  $N_e/N$  in salmon populations.

The extent to which variance in reproductive success plays an important role in determining  $N_e/N$  in other organisms remains largely unknown. However, recent studies indicate that its role can be substantial. For example, Turner *et al.* (2002) showed that variance in reproductive success is largely responsible for very small  $\hat{N}_e/\hat{N}$  (= 0.001) in red drum (*Sciaenops ocellatus*), whereas Matocq (2004) showed a moderately large  $\hat{N}_e/\hat{N}$  (= 0.48) in a woodrat (*Neotoma macrotis*) population that has low variance in reproductive success ( $V_k \sim \bar{k}$ ) despite their population structure of harem polygyny.

*Genetic compensation between life-history forms*

In the Hood River steelhead, it appears that nonanadromous fish play an important role in stabilizing  $N_b$  and maintaining a high  $N_e/N$ , despite the variable census sizes of anadromous adults. The negative correlation between anadromous run size and inferred reproductive contribution of nonanadromous parents (Fig. 5) is most likely caused by a genetic compensation between life-history forms, in which a stable population of nonanadromous parents contributes a relatively constant number of offspring to the anadromous population every year. Another potential explanation for the relationship we observed is an increased competitive ability of nonanadromous parents in the spawning ground when the number of anadromous competitors is small. In this case, an increase in the absolute (rather than relative) contribution of nonanadromous parents to the anadromous populations is expected when anadromous run size is small. We did not detect any statistical evidence of negative correlation between the anadromous run size and the (inferred) absolute contribution of nonanadromous parents from our data (two-tailed *t*-test,  $P > 0.40$ ), whereas the correlations tended to be negative ( $r = -0.49$  to  $-0.03$ ). This result indicates that the genetic compensation between life-history forms is primarily due to stable numbers of contributing nonanadromous parents, although a possibility of the increased competitive ability of nonanadromous parents remains.

A negative correlation between  $N_e/N$  and  $N$  has been reported in Atlantic salmon (Fraser *et al.* 2006), an insect (Pray *et al.* 1996), and a plant (Husband & Barrett 1992), suggesting that genetic compensation is a common mechanism for the maintenance of genetic diversity. Given that many organisms have different life-history forms with different reproductive strategies within species (Clutton-Brock 1988), genetic compensation between life-history forms might also be common. In Atlantic salmon, for instance, a potentially important role of sexually matured parr on  $N_e$  is suggested (Jones & Hutchings 2002). As a practical consequence, conservation programmes that focus only on a part of life-history forms may not be sufficient to maintain genetic diversity throughout the entire populations. Our results emphasize the need to support the full range of diversity, including life-history polymorphisms.

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