ORIGINAL PAPER

Stocking of captive-bred fish can cause long-term population decline and gene pool replacement: predictions from a population dynamics model incorporating density-dependent mortality

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Received: 17 August 2010 / Accepted: 15 April 2011 / Published online: 5 May 2011 © Springer Science+Business Media B.V. 2011

Abstract Releasing captive-bred fish into natural environments (stocking) is common in fisheries worldwide. Although stocking is believed to have a positive effect on fish abundance over the short term, little is known about the long-term consequences of recurrent stocking and its influence on natural populations. In fact, there are growing concerns that genetically maladapted captive-bred fish can eventually reduce the abundance of natural population. In this study, we develop a simple model to quantitatively investigate the condition under which recurrent stocking has long-term effects on the natural population. Using a population dynamics model that takes into account a density-dependent recruitment, a gene responsible for the fitness difference between wild and captive-bred fish, and hybridization between them, we show that there is little or no contribution of recurrent stocking to the stock enhancement without a replacement of the wild gene pool by the captive-bred gene pool. The model further predicted that

Electronic supplementary material The online version of this article (doi:10.1007/s12080-011-0128-y) contains supplementary material, which is available to authorized users.

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Department of Fish Ecology and Evolution, Swiss Federal Institute of Aquatic Science and Technology (EAWAG), Center of Ecology, Evolution and Biogeochemistry, Seestrasse 79, 6047 Kastanienbaum, Switzerland stocking of an intermediate level causes a reduction, rather than enhancement, of population size over the long term. The population decline due to stocking was attributed to the fitness disadvantage of captive-bred fish and strong overcompensation at recruitment stage. These results suggest that it would be difficult to simultaneously attain population size recovery and conservation of the local gene pool when captive-bred fish have fitness disadvantage in the wild, although caution is needed when applying the predictions from the simplified model to a specific species or population.

Keywords Stocking · Fish · Supplementation · Population dynamics · Genetic effect · Harvest

Introduction

The sustainable management of endangered species is a central issue in conservation biology. The release of captive-bred organisms is one of the most popular methods of restoring populations that have declined, especially culturally and economically valuable species such as cheetah in Africa and salmon in northern rivers (Olney et al. 1994; Knudsen 2000). Because many wild animal populations are declining, the demand for captive breeding programs is increasing (Pimm and Raven 2000; Ceballos and Ehrlich 2006; Frankham et al. 2010).

Releasing captive-bred fish into natural environments (hereafter, "stocking") is a widespread practice in fisheries. Stocking programs have been operated not only for supporting fisheries but also for conservation purposes. Stocking is believed to be a major contributor to fisheries production and stock enhancement worldwide (Leber and Blankenship 1995; Welcomme and Bartley 1998; Kitada and Kishino 2006). Enhancement of fish populations by stocking, however, is one of the most controversial approaches to fisheries management (Brannon et al. 2004; Hilborn 2004; Fraser 2008). Stocking can, at least in some cases, benefit fisheries by increasing the catch of desirable fish and the capital value of the fishery in the short term (Kitada and Kishino 2006; Berejikian et al. 2008). However, there are risks associated with the practice: stocking itself may not be successful in terms of stimulating the population size (Svåsand et al. 2000; Araki and Schmid 2010); it may give rise to ecological competition between wild and captive-bred individuals (Nickelson 2003) and it could impact other species in the ecosystem, including those that may have conservation value (Saura et al. 1990; Holmlund and Hammer 1999). The ecological competition might induce a density-dependent mortality, which can lead the stocked population to a net loss in the number of naturally spawned fish (Goodman 2005). Indeed, such a density-dependent mortality due to stocked fish is reported in a chinook salmon population (Levin et al. 2001).

Another concern is that when released fish interbreed with local wild stocks, they might alter the genetic composition of the locally adapted population and reduce the genetic diversity and population viability of wild stocks (Ryman and Laikre 1991; Lynch and O'Hely 2001; Ford 2002; Araki et al. 2009). Genetic changes in captive-bred organisms that reduce fitness in the wild have been reported (Reisenbichler and Rubin 1999; Araki et al. 2007, 2008; Williamson et al. 2010).

The long-term ecological effects of stocking are difficult to monitor, because changes in genetic composition and population size tend to occur very slowly (Mooney et al. 1995; Holling et al. 1998). Another problem is a technical difficulty in developing appropriate controls to evaluate the stocking effects. One way to increase understanding of the impacts of recurrent stocking is to develop a population dynamics model that explicitly incorporates demographic and genetic processes between wild and captive-bred fish. For example, Ford (2002) combined quantitative genetic model and demographic model to explore the effects of selection on the fitness of a supplemented population and showed that substantial phenotypic changes and fitness reduction can occur even if a large fraction of the captive broodstock is brought from the wild every generation. Other models have been presented to examine the fitness consequences of genetic difference between wild and captive-bred populations (Hutchings 1991; Lynch and O'Hely 2001; Hindar et al. 2006). These previous models, however, do not fully address the two potential pathways by which stocking can influence the natural populations at the same time: genetic effect of captive breeding and the density-dependent mortality in the wild.

In this study, we further develop the theoretical model in which the long-term consequences of recurrent stocking on the abundance and the genetic composition of a natural population are simultaneously investigated. In particular, we compare the Ricker and the Beverton-Holt models to explore the impact of different type of density dependence on stock enhancement. Combining a population dynamics model with a one-locus two-allele model for selection, we ask under what conditions stocking can contribute to stock enhancement in the long run. In addition, we monitor the changes in genetic composition of the population asking whether the intermediate levels of stocking allow the population enhancement without a replacement of the wild gene pool with the captive-bred gene pool over the long term. Our result suggests that it would be difficult to simultaneously attain population size recovery and conservation of the local gene pool. We also found that in the Ricker-type model, severe overcompensation in density-dependent recruitment resulted in a decline in the average population size even when there is no selective disadvantage of captive-bred genotypes while such a population decline was not predicted in the Beverton-Holt model. This result implies that stocking would cause stronger negative impacts on fish populations when overcompensation is greater. Although we mainly focus on a simple one-locus two-allele model, the main conclusion was further confirmed by two-loci model as well (Supplementary material 1 in the Electronic supplementary material (ESM)).

The model

In this study, we consider a model of female population dynamics in a single fish species. The presence of males is ignored in the population dynamics, but an equal sex ratio with regard to genotype (see below) is assumed during the mating phase. Two developmental stages, juvenile and adult, are considered in this model. See Table 1 for glossary of notations. As for the genetic part of the model, we considered a one-locus two-allele model by which the fitness difference between wild and captive-bred fish is determined.

Population dynamics of wild fish with no stocking

We first developed the population dynamics of wild fish when no stocking occurs. We assume the following basic life cycle of the fish species. Once a year, the female deposits eggs, which develop and hatch. Fry grow and become juveniles and adults, and then adults spawn. With the assumption of clear seasonality in the life cycle, the temporal dynamics of the wild populations of juvenile and

Table 1 N	otations in	the study	and default	values	of p	parameters
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x_W	Number of juvenile females with wild genotype	
x_H	Number of juvenile females with hybrid genotype	
x_C	Number of juvenile females with captive-bred genotype	
\mathcal{Y}_W	Number of adult females with wild genotype	
y_H	Number of adult females with hybrid genotype	
УС	Number of adult females with captive-bred genotype	
N	Population size $(=y_W + y_H + y_C)$	
S_W	Survival probability of wild genotype per year	0.4
S_H	Survival probability of hybrid genotype per year	
s_C	Survival probability of captive-bred genotype per year	
μ	Maturation probability per year	0.5
r	Intrinsic population growth rate at a juvenile stage	
Κ	Environmental carrying capacity for recruitment	100
и	Survival probability of stocked fish in the stocked year	0.6
S	Number of stocked fish per year	
q	Proportion of harvest per year	0.1
p_W	Proportion of wild genotype	
p_H	Proportion of hybrid genotype	
p_C	Proportion of captive-bred genotype	
ε	Fitness disadvantage of captive-bred genotype	0.5
h	Degree of dominance in the fitness trait	0.5

adult females, denoted by x_W and y_W , respectively, are given by the following discrete-time dynamics:

$$x_W(t+1) = s_W(1-\mu)x_W(t) + y_W(t)e^{r\left[1-\frac{y_W(t)}{K}\right]},$$
 (1a)

$$y_W(t+1) = s_W(\mu x_W(t) + [1-q]y_W(t)).$$
(1b)

The first term on the right-hand side of Eq. 1a represents the fraction of juvenile wild fish that have survived and have not reached the adult stage within a year. s_W and μ represent the survival probability per year of wild fish and the maturation probability, respectively. $1/(1-s_W)$ and $1/\mu$ represent average longevity and average maturation time. The second term on the right-hand side of Eq. 1a denotes recruitment. Recruitment is defined as the number of individuals that reach the juvenile stage. We first assume the Ricker-type stock-recruitment relationship (Ricker 1954). The Beverton-Holt model will be analyzed in "Different functional type: Beverton-Holt model." The Ricker function leads to overcompensation where high spawner abundance leads to low recruitment. Cannibalism is one of such examples (Dong and DeAngelis 1998). The Ricker model is commonly used to model time-series data from density-dependent fish populations (Myers et al. 1999; Krkošek et al. 2007). r and K are the population growth rate at the juvenile stage and the environmental carrying capacity for recruitment, respectively. r/K determines the density-dependent mortality at the recruitment stage. The population size of adult wild fish in year t+1, $y_W(t+1)$, is composed of two terms (Eq. 1b): the fraction of juveniles that have matured to adulthood ($s_W \mu x_W(t)$) and the fraction of adults that have survived without being harvested ($s_W[1-q]y_W(t)$). q represents the proportion of harvest per year, which is a product of catchability and harvesting effort per year and is a constant (independent of age) in this study.

Population and genotype dynamics under stocking

When stocking takes place, dynamics of the wild fish population are affected (Fig. 1). We assume that the stocked fish are genetically different from the wild fish and that interbreeding between the two types of fish occurs to create hybrids. For simplicity, we first consider a one-locus, two-allele model to investigate the genetic impacts of stocking on population dynamics. In this model, three genotypes-wild (W), hybrid (H), and captive bred (C)-emerge depending on genetic origin (Fig. 1). W and C represent individuals that are homozygous for wild and hatchery origin alleles, respectively, and H represents heterozygotes. The one-locus simulation model for fish stocking that considers no densitydependent competition was previously studied by Ryman (1997). To confirm the generality of our results, we also examined a two-loci model in Supplementary material 1 in the ESM, and found that overall conclusion did not differ between the two models.

The terms y_W , y_H , and y_C represent the adult population sizes of wild, hybrid, and captive-bred female fish, respectively; in other words, the number of adult females carrying the W, H, and C genotypes. Assuming there is random mating, each female mates with the three types of males with a probability equal to their encounter probabilities, i.e., $p_W = y_W/(y_W + y_H + y_C)$ for the wild type, $p_H = y_H / (y_W + y_H + y_C)$ for the hybrid type, and $p_c =$ $y_C/(y_W + y_H + y_C)$ for the captive-bred type. p_W , p_H , and y_C also represent genotype frequencies in the population. When a wild-type female mates with a wild-type male, the female produces only wild-type offspring. When a wild-type female mates with a hybrid-type male, a 1:1 ratio of wild- and hybrid-type offspring is produced because of Mendelian inheritance of the "captive-bred gene." When a wild-type female mates with a captivebred-type male, the female produces only hybrid-type offspring. When hybrid-type female mates with a hybridtype male, 1:2:1 ratio of wild-, hybrid-, and captive-bredtype offspring is produced. By applying the same argument to the other types of females, we find that the temporal population dynamics of juveniles of the wild



type (x_W) , hybrid type (x_H) , and captive-bred type (x_C) are given by the following:

$$x_{W}(t+1) = s_{W}(1-\mu)x_{W}(t) + \left[\left(p_{W}(t) + \frac{p_{H}(t)}{2}\right)y_{W}(t) + \frac{1}{2}\left(p_{W}(t) + \frac{p_{H}(t)}{2}\right)y_{H}(t)\right]\phi(t),$$
(2a)

$$x_H(t+1) = s_H(1-\mu)x_H(t) + \left[\left(\frac{1}{2}p_H(t) + p_C(t)\right)y_W(t) + \frac{y_H(t)}{2} + \left(p_W(t) + \frac{1}{2}p_H(t)\right)y_C(t)\right]\varphi(t),$$
(2b)

$$x_{C}(t+1) = s_{C}(1-\mu)x_{C}(t) + \left[\frac{1}{2}\left(\frac{p_{H}(t)}{2} + p_{C}(t)\right)y_{H}(t) + \left(\frac{p_{H}(t)}{2} + p_{C}(t)\right)y_{C}(t)\right]\varphi(t) + uS,$$
(2c)

where

$$\varphi(t) = e^{r \left[1 - \frac{y_W(t) + y_H(t) + y_C(t)}{K}\right]}.$$
(2d)

 s_W , s_H , and s_C are the annual survival probabilities of wild-, hybrid-, and captive-bred-type fish. $\varphi(t)$ represents densitydependent recruitment. In this model, all emergent fish equally contribute to density-dependent recruitment regardless of their genotype. The difference between the nostocking situation considered in Eqs. 1a and 1b and the stocking situation considered in Eqs. 2a-2d is the addition of a stocking term, uS, in Eq. 2c and the resultant hybridization between wild and stocked fish. u and S are the survival probability and amount of stocked fish, respectively. We assume that stocking takes place after density regulation, i.e., stocked fry have a densityindependent survival probability. In addition, we assume a lower survival probability of captive-bred type in the wild, but the maturation probability is the same among the genotypes. u and s_C would be different because different factors (such as predation and disturbances during newly stocked fry settle into new habitats) influences mortality. We examined different assumptions regarding reproductive contributions of different genotypes in Supplementary material 2 in the ESM.

Assuming that the annual survival probability is independent of age and that there is no difference in the proportion of harvest of the various genotypes, we can determine the population sizes of adult fish of wild, hybrid, and captive-bred types, denoted by y_W , y_H , and y_C , by the following;

$$y_W(t+1) = s_W(\mu x_W(t) + [1-q]y_W(t)),$$
(3a)

$$y_H(t+1) = s_H(\mu x_H(t) + [1-q]y_H(t)),$$
 (3b)

$$y_C(t+1) = s_C(\mu x_C(t) + [1-q]y_C(t)).$$
(3c)

Poor survival probabilities among stocked juveniles have been reported, especially in environments with low carrying capacities and with native reproductive populations (e.g., Reisenbichler and McIntyre 1977; Morán et al. 1991; Hansen et al. 1993; Fleming et al. 2000). The survival probability of hybrids is likely between the survival probabilities of the two homozygote genotypes (McGinnity et al. 2003; Araki et al. 2009). Thus, we apply a general model in which the relative survival probabilities of wild, hybrid, and captive-bred types are 1, $1-h\varepsilon$, and $1-\varepsilon$, respectively. ε and h represent the fitness disadvantage of the captive-bred type and a degree of dominance $(0 \le h \le 1)$, respectively. For instance, h=0 represents complete dominance of the wild type; h=0.5 represents no dominance; and h=1 is for which the wild type is completely recessive. Therefore, survival probabilities of the hybrid and captive-bred types are given as $s_H =$ $s_W(1-h\varepsilon)$ and $s_C = s_W(1-\varepsilon)$, respectively. Stochastic multi-locus simulations that adopt similar assumption were studied by Theodorou and Couvet (2004). Note that in this study, we distinguish between the three types of fish based solely on their fitness-determining genotypes, regardless of the rest of the genome that could have different origins due to recombination.

Results

Population dynamics of wild fish with no stocking

We first give a brief overview of wild fish population dynamics under an assumption of no stocking. We then analyze how stocking alters wild fish population dynamics. From Eqs. 1a and 1b, the equilibrium population sizes of juveniles (x_W^*) and adults (y_W^*) of wild fish were derived as follows;

$$x^{*}_{W} = \frac{K}{s_{W}\mu} (1 + s_{W}q - s_{W})(1 - \log A/r), \tag{4}$$

$$y_W^* = K(1 - \log A/r),$$
 (5)

where $A = \frac{1}{s_W\mu} (1 + s_W\mu - s_W)(1 + s_Wq - s_W)$. Thus, the population size of both juvenile and adults at equilibrium increases as carrying capacity *K* and population growth rate at a juvenile stage *r* increase.

The overcompensation in the stock-recruitment relationship assumed in the Ricker curve generates oscillation because of instability in the equilibrium point (Ricker 1954). We illustrated the diverse population dynamics in a bifurcation plot (Fig. 2). The bifurcation was plotted as follows: for each value of parameter r, population dynamics were simulated for 10,250 time steps. The first 10,000 time points were discarded because the population may not have reached asymptotic behavior during this period (however, see Supplementary material 3 in the ESM for discussion). Population sizes for the remaining 250 time points were plotted against r. Bifurcation diagram did not change even when we discarded longer time points as transient. When the population growth rate at a juvenile stage was low, the population size converged to the equilibrium given in Eq. 4. The population dynamics switched from stable to periodic or chaotic oscillation according to increases in population growth rate at a juvenile stage (Fig. 2). The bifurcation point at which the system switches from stable to unstable (illustrated by an arrow in Fig. 2) can be determined by analyzing the Jury condition. The result shows that bifurcation occurs at $r = \frac{2(1-s_W)+s_W(q+\mu+\mu A \log A)}{s_W \mu A}$. In the next section, we see how these population dynamics were altered by stocking.



Fig. 2 Bifurcation diagram of wild-type fish population dynamics with no stocking along the population growth rate at a juvenile stage r

Population and genotype dynamics under stocking

We assumed that a constant number of juveniles were being stocked per year. Due to an additional term for stocking in Eq. 2c, the coupled dynamics of wild, hybrid, and captivebred fish abundance were not solvable. We thus performed numerical calculations of Eqs. 2a–2d and 3a–3c and summarized the results for 250 years after the first 10,000 years were discarded as transient. Even though we focused on the long-term consequences of recurrent stocking in this study, the changes can occur in the contemporary time scale (see Supplementary material 3 in the ESM). When r=1.0, the wild-type genotype decreased as the number of stocked fish increased (Fig. 3a), causing a gradual replacement of the wild genotype with hybrid and captivebred genotypes (Fig. 3b, c). Wild and hybrid genotypes decreased as the stocking further increased (Fig. 3a, b) and finally the entire population was replaced with the captivebred genotype (Fig. 3c). Even when we assumed larger r with oscillation, similar pattern was observed (e.g., r=5.0; Fig. 3d–f). The replacement of wild genotype by captivebred genotype occurred with a small amount of stocking when r is low (compare Fig. 3a–c and d–f).

Our model demonstrated that stocking does not necessarily result in an increase in the population size and net



Fig. 3 Population size of wild- (a, d), hybrid- (b, e), and captive-bred-type fish (c, e) under recurrent stocking. a-c Population growth rate at a juvenile stage r=1.0. d-f r=5.0

harvest. We plotted the temporal average of adult population size, $\overline{N} = \sum_{t=0}^{T-1} [y_W(t) + y_H(t) + y_C(t)]/T$, against the relative abundance of stocked fish to the carrying capacity of the population (i.e., the *S/K* ratio). *T* represents time for evaluation (in years), and is 250 in this study. The net harvest over the long term was in proportion to the average population size and was denoted by $q\overline{N}$, where *q* is the proportion of harvest introduced in Eqs. 1b, and 3a–3c. Under the range of parameters we investigated, the results were unchanged as long as \overline{N} and *S* were measured by the unit of *K*. Thus, we used the *S/K* ratio as an indicator to measure the impacts of stocking on stock enhancement and genetic composition.

 \overline{N} first decreased gradually as the *S/K* ratio increased, and the minimum average population size was attained at a certain magnitude of the *S/K* ratio (Fig. 4a and arrows in b). After the average population size reached its minimum, the decreasing trend turned to an increasing one (Fig. 4b). We call the value of the *S/K* ratio where this transition occurred the "threshold *S/K* ratio." The threshold *S/K* ratio increased as the population growth rate at a juvenile stage *r* increased (Fig. 4c), meaning that in a population with a higher population growth rate at a juvenile stage, a higher level of stocking was needed to enhance the population size and net harvest.

The shift in this demographic trend coincided with the replacement of the wild genotype by the captive-bred genotype (Fig. 5), implying that the wild-type gene pool would be largely lost once stocking began contributing to stock enhancement. The mean of natural recruitment rate of the captive-bred genotype had a peak around the turning point when r=5 (thin dashed line in Fig. 5e) and rapidly decreased to almost 0 with an increase in the S/K ratio. This implies that the enhancement in population size caused by large amounts of stocking is attributable only to the stocking itself, and natural recruitment of stocked fish rarely occurs in this condition. The replacement of the wild genotype by the captive-bred genotype was observed at or above the threshold S/K ratio under any parameter sets we investigated (see Supplementary materials 4-7 in the ESM).

We compared the average population size realized at the threshold S/K ratio (hereafter, "minimum," as this is the minimum population size across stocking levels) with the original population size without stocking (hereafter, "original"). The decline in average population size due to stocking did not occur when r was very small (Fig. 6). However, when the captive-bred genotype was under a significant disadvantage compared with the wild genotype (ε =0.25 and 0.75), the minimum could be as small as 10% of the original with a population growth rate at a juvenile stage r that was close to unity (Fig. 6). When



against the relative abundance of stocked fish (S) to the carrying capacity of the population (K). *thick solid line*, ε =0.75; *thin solid line*, ε =0.25; *dashed line*, ε =0.0. Population growth rate at a juvenile stage r=5.0. **b** Average population size against the relative abundance of stocked fish (S) to the carrying capacity of the population (K). *Thick solid line*, r=5.0; *thin solid line*, r=2.0; *dashed line*, r=1.0. *Arrows* indicate the threshold S/K ratio for each *line*. **c** Threshold S/K ratio against population growth rate at a juvenile stage r. *Thick solid line*, fitness disadvantage of the captive-bred genotype ε =0.75; *thin solid*

line, ε =0.25; *dashed line*, ε =0.0. *q*=0 was used for (c)





captive-bred fish had no fitness disadvantage ($\varepsilon = 0$), such a reduction of average population size around small magnitude of r was not observed (dashed line in Fig. 6). This result implies that heritable fitness disadvantage in the captive-bred genotype is a major factor that causes declines in the average population size due to stocking when the effect of overcompensation in density-dependent recruitment is weak.

If the selective disadvantage of captive-bred genotypes is the only reason that average population size decreases, we would expect no reduction in population size when there is no fitness disadvantage for captive-bred genotypes (i.e., $\varepsilon =$ 0.0). However, even when $\varepsilon = 0.0$, the decline in average population size occurred when the population growth rate at a juvenile stage r was significantly large (It is larger than the bifurcation point given in "Population dynamics of wild fish with no stocking," and thus the system shows oscillation).

An alternative mechanism for explaining a declining population size when $\varepsilon = 0.0$ is strong overcompensation. Stocking (uS) results in an increment of adult fish by $s\mu uS/\{1-s(1-\mu)\}$ on average. This increment escalates overcompensation, which results in a further reduction in the amount of natural recruits (dashed line in Fig. 7a). Because the reduction by elevated overcompensation exceeds the increment by stocking on average, the average



Fig. 6 Change in percent minimum average population size to original population size without stocking along the population growth rate at a juvenile stage *r*. *Thick solid line*, fitness disadvantage of the captive-bred genotype ε =0.75; *thin solid line*, ε =0.25; *dashed line*, q=0 was used for calculation

population size decreases. As the S/K ratio increased, a reduction in natural recruits caused by severe densitydependent mortality was compensated for by artificial recruitment, and the population trend then turned from



Fig. 7 Plot of average population size $\overline{N} = \sum_{t=0}^{T-1} [y_W(t) + y_H(t) + y_C(t)]/T$ (*thick solid line*), mean of natural recruitment by captive-

bred genotype (*dashed line*), mean of natural recruitment by captivebred genotype (*dashed line*), and mean of artificial recruitment by stocking (*thin solid line*) along the relative abundance of stocked fish (*S*) to the carrying capacity of population (*K*). **a** r=7.0. **b** r=2.0. $\varepsilon=0.0$ and q=0 were used for calculation

decreasing to increasing. When the population growth rate at a juvenile stage was low (such as r=1.0 or 2.0), a decline in average population size did not occur as long as there is no selective disadvantage of captive-bred genotypes (i.e., $\varepsilon=0.0$), because the artificial recruitment by stocking always exceeded the reduction in natural recruitment when overcompensation is not sufficiently strong (i.e., r is small) (Fig. 7b). The reduction of average population size due to stocking under no fitness disadvantage of captive-bred genotype was not predicted in the Beverton–Holt model that does not exhibit overcompensation as we explain in "Different functional type: Beverton–Holt model."

Effects of the other parameters are summarized as follows. The degree of dominance of the captive-bred genotype (h) had almost no effect on the average population size, although h affected the timing of the replacement of the wild genotype by the captive-bred genotype (Fig. 4 in the ESM). The proportion of harvest (q), the survival probability of stocked juveniles (u), and maturation probability (μ) influenced the magnitude of the threshold S/K ratio and the timing of the replacement of the wild genotype by the captive-bred genotype (Figs. 5-7 in the ESM). However, the overall trends outlined above were conserved among the different parameter sets. Even though we emphasized the long-term consequences of recurrent stocking in this study, we found that the decline in average population size and the replacement of the wild gene pool occur within the contemporary time scale (Supplementary material 3 in the ESM).

Different functional type: Beverton-Holt model

The decline in the average population size due to stocking occurred even when we applied a different stock-recruitment relationship; in the Beverton-Holt model (Beverton and Holt 1957), for example, Ricker-type densitydependent effect formalized in Eq. 2d is replaced by $\varphi(t) = a/\{1 + b(y_W(t) + y_H(t) + y_C(t))\}$. a and b are control parameters, and (a-1)/b equivalents to the carrying capacity K for recruitment. By applying the new function, we numerically recalculated Eqs. 2a-2d and 3a-3c and plotted the average population size along S/K ratio (Fig. 8a). It is clearly shown that the decline in the average population size happened when captive-bred genotypes is selectively disadvantageous to wild genotypes (i.e., positive ε). This decline is consistent to the conclusion derived from the analysis of the Ricker-type model; heritable fitness disadvantage in the captive-bred genotype is a major factor that causes declines in the average population size due to stocking when the effect of overcompensation in densitydependent recruitment is weak. In the Ricker-type model, severe overcompensation in density-dependent recruitment also resulted in a decline in the average population size Fig. 8 Beverton–Holt-type stock–recruitment relationship. **a** Average population size $\overline{N} = \sum_{t=0}^{T-1} [y_W(t) + y_H(t) + y_C(t)]/T$ against the relative abundance of stocked fish (*S*) to the carrying capacity of the population (*K*). Thick solid line, ε =0.75; thin solid line, ε =0.25; dashed line, ε =0.0. **b** Genotype frequency of wild type. **c** Genotype frequency of hybrid type. **d** Genotype frequency of captive-bred type.

Other parameters are a=11, b=0.1, and $\varepsilon=0.75$

even when there is no selective disadvantage of captivebred genotypes (i.e., ε =0.0). However, the decline never happened in the Beverton–Holt model when ε =0.0. An imbalance between reduction in natural recruitment and artificial recruitment illustrated in Fig. 7a does not occur in the Beverton–Holt model when ε =0.0, because overcompensation never occurs and a reduction of natural recruitment is always compensated by an increment by artificial recruitment. This result is a critical difference caused by different functional type used for stock–recruitment relationship. On the other hand, the gene pool replacement of wild genotype by captive-bred genotype always occurred when stocking had notable contribution to the population abundance regardless of the magnitude of selective disadvantage (e.g., Fig. 8b–d).

Stocking release before density-dependent competition

We examined different assumptions regarding the timing of stocking release. In the original model, stocking was assumed to occur after density-dependent competition. In this section, we assumed that stocking is took place at an earlier stage before density-dependent competition. To reflect the density-dependent competition on stocked fish at the year of stocking, Eqs. 2c and 2d were modified as

$$x_{C}(t+1) = s_{C}(1-\mu)x_{C}(t) + \left[\frac{1}{2}\left(\frac{p_{H}}{2}+p_{C}\right)y_{H}(t) + \left(\frac{p_{H}}{2}+p_{C}\right)y_{C}(t) + \frac{S}{\lambda}\right]\varphi'(t),$$
(6)

$$\varphi'(t) = \lambda e^{\left[-\frac{\lambda\left(y_{W}(t)+y_{H}(t)+y_{C}(t)\right)+S}{K}\right]},$$
(7)

where $\lambda = e^r$. $\varphi(t)$ in Eqs. 2a and 2b is also replaced by $\varphi'(t)$ in this new model. Because stocked fry do not reproduce, *S* should be discounted by λ . When we modified the model to allow stocking at an earlier stage, after which stocked juveniles would experience density-dependent competition in the wild, the model predicted that most stocked juveniles would not survive to maturation, and the entire population often went almost extinct (Fig. 9). This result may provide a possible management implication in terms of adjusting the timing (life history stage) of release of stocked fish to mitigate negative effects of stocking.





Fig. 9 Effects of stocking release before density-dependent competition on average population size \overline{N} . The other parameters are r=3.0, K=100, $\mu=0.5$, u=0.5, q=0, $\varepsilon=0.5$, h=0.5, and $s_W=0.4$

Discussion

In this study, we developed a population dynamics model to address the effects of fish stocking on stock enhancement and genetic composition. We focused our analysis on the long-term capability of recurrent fish stocking to increase the population size and on the risk of replacement of the wild gene pool with the captive-bred gene pool. The main conclusion of this study is that recurrent stocking does not contribute to stock enhancement without the replacement of wild genotypes by captive-bred genotypes. Reducing the amount of stocking naturally lower the risk of replacement, but the model further predicted that intermediate levels of stocking often have an unexpected and undesirable consequence: a decline in the average population size, and hence a decrease in net harvest over the long term.

Causes of the decline in average population size due to stocking

There are two reasons for the decline. The first concerns the fitness disadvantage conferred by the captive-bred genotype compared with the wild genotype in natural environments. Under stocking, hybrid or captive-bred genotypes replace wild genotypes in a certain fraction of the carrying capacity of a habitat. If hybrid and/or captive-bred genotypes have lower fitness than the wild genotype (positive ε), and if the fitness difference is genetically based (Morán et al. 1991; Araki et al. 2007), then this selective disadvantage results in a decline in the overall population size, and consequently the harvest decreases (Figs. 5 and 6). The heritable effect of captive breeding that reduces the wild population fitness is reported empirically, even when the stocking is meant for conservation and local wild fish are used as broodstock (Araki et al. 2009). Previous theoretical studies have also pointed out the increased genetic load on wild population

caused by the introduction of captive population (Hutchings 1991; Lynch and O'Hely 2001; Ford 2002; Hindar et al. 2006). For example, Ford (2002) used quantitative genetic model to explore the fitness consequences of a single quantitative trait under stabilizing selection for different phenotypic optima in two infinite subpopulations. Lynch and O'Hely (2001) modeled the situation in which a natural population is exposed to recurrent introductions from a captive population where selection against deleterious allele is somewhat relaxed. Although our model is different from these previous models in terms of stage structure and density-dependent mortality, the theoretical prediction about the fitness load caused by stocking is qualitatively similar to those reported previously. This suggests that our results are not a particular feature of one specific model but rather a general outcome. In some respects, these results are related to theory concerned with the migration load (see Lenormand 2002 for review) because similar patterns for decrease in mean fitness of a population are caused by immigration.

In addition to the increased genetic load, we found another reason for the population decline, the strong density-dependent competition at the recruitment stage. Stocking enhances the population size of the captive-bred genotype over a short time period, and an increase in adult fish induces stronger overcompensation at natural recruitment stage when the population growth rate at a juvenile stage is high. This causes a significant reduction in natural recruits, enhances the extinction of wild genotype, and precipitates the decline in the average population size (Figs. 6 and 7; note that the population size fluctuates heavily over time under strong overcompensation). Such effect was not observed in the Beverton-Holt model in which overcompensation does not occur, implying that strong overcompensation is a major factor for the population decline. This result means that stocking would cause stronger negative impacts on fish populations when overcompensation is greater.

Comparison between Figs. 4a and 8a allows us to quantify the relative effects of fitness disadvantage and overcompensation on the population decline. The line with $\varepsilon = 0$ in Fig. 4a quantifies the contribution of overcompensation alone, while the lines with positive ε in Fig. 8a quantify the contribution of fitness disadvantage alone. The joint effects of fitness disadvantage and overcompensation are represented by the lines with positive ε in Fig. 4a, and the population decline was the largest in this situation. In Supplementary material 8 in the ESM, we showed that the interaction between fitness disadvantage and overcompensation contributes to mitigate population decline when r is larger than the bifurcation point. A smaller population size due to strong fitness disadvantage would reduce the level of overcompensation on average, leading

to a smaller decline of mean population size. Such an interaction disappeared as the population growth rate increases, and it had little influence on the overall pattern of the relationship between population abundance and stocking amount (Figs. 4a and 8a).

These results suggest that the consequences of stocking might contradict the original purpose of the stocking program and refute the belief that stocking contributes to stock enhancement. Stocking programs for conservation are even more controversial because our model indicates that population size increases due to stocking cannot be achieved without the replacement of the local gene pool with a potentially less fit captive-bred genotype. Hatchery managers of stocking programs usually have two goals: to increase fish stocks and to conserve wild fish populations (Waples and Drake 2004). Our model clearly shows that a trade-off exists between stock enhancement and the conservation of wild gene pool and that it would be impossible to realize these two goals simultaneously because an increase in population size due to stocking is likely only when the wild gene pool has already been replaced by the captive-bred genotype.

Limitations and general applicability of the model predictions

How generally can we apply our model predictions to other systems and taxa? We acknowledge that the model we used in this study is simple and based on many assumptions. Thus, the applicability of our conclusions to actual stocking programs, including ones for other species should be considered carefully. For instance, we assumed specific timing for stocking: juveniles were stocked at a later stage to avoid density-dependent competition among juveniles, and thus they were not subject to this competition until they spawned in the wild. When we modified the model to allow stocking at an earlier stage, after which stocked juveniles would experience density-dependent competition in the wild, the model predicted that most stocked juveniles would not survive to maturation, and the entire population often went extinct.

Density-dependent competition among stocked juveniles might occur when the juveniles stay long around where they are stocked and when the carrying capacity of the local environment is low (e.g., freshwater species in a tributary of a river; Morán et al. 1991; Hansen et al. 1993). On the other hand, when captive-bred population is constantly reconstructed from wild genotype individuals (not from wild "population," because the wild population can be dominated by captive-bred genotype after recurrent stocking), the proportion of gene pool replacement will be lower and the negative fitness effect of captive breeding might be weaker than observed in this study (Lynch and O'Hely 2001). In addition, the population size decline due to stocking by the second reason, the severe density-dependent competition at the recruitment stage, will not occur when there is no overcompensation in the recruitment. Furthermore, our model predicts that when intrinsic population growth rate is small (r < 1), wild populations cannot most likely be selfsustained, and hence recurrent stocking might be an only practical option despite the gene pool replacement in the long run (Fig. 3). Indeed, there are a few examples showing that captive breeding programs helped a recovery of declining populations from the brink of extinction (e.g., California condor and black-footed ferret) (Snyder and Snyder 1989; Miller et al. 1994; Frankham et al. 2010). Thus, in some cases, we believe that captive breeding program can still be a useful tool for preservation and recovery of an otherwise declining population in the short term.

Another limitation might stem from our assumption of a single gene to represent the genetic effect for simplicity. However, the fact that the two-loci model in Supplementary material 1 in the ESM and even a more realistic, quantitative genetic model in a previous study (Ford 2002) showed similar results suggests that our conclusion of the potential population decline due to recurrent stocking in this study does not depend on this assumption. While we know little about the genetic architecture of fitness traits in fish, a strong effect of single gene on the fitness of individuals has been reported in both animals and plants (Abzhanov et al. 2006; Shindo et al. 2008; Árnason et al. 2009).

Despite the limitations above, three lines of evidence suggest that our predictions might be applicable to many captive breeding programs for stock enhancement: first, our conclusions remained valid in wide ranges of parameters. The tested parameters include population growth rate at a juvenile stage, maturation, survival probabilities, proportion of harvest and the degree of dominance (Figs. 4-7 in the ESM and Fig. 3a); second, the main conclusions were robust against the modifications of the model and changes in assumptions (Figs. 1-3 in the ESM and Fig. 8). The decline of population size due to stocking we observed was also consistent with previous theoretical studies, in which maladaptation of a quantitative trait in stocked individuals was linked to population dynamics and fitness (Tufto 2001; Lynch and O'Hely 2001; Ford 2002). The consistency of the results among different models indicates that the observed pattern is not model specific; Finally, our results are consistent with the fact that there is scant evidence for recurrent stocking programs to cause a steady recovery of declined population in a variety of taxa, including fish species (Fraser 2008; Araki and Schmid 2010). Thus, with cautions above, a simple and mechanistic model will be a useful tool to assess long-term performance of potential stocking programs in general.

Acknowledgments This work was supported by the 2007 special coordination funds for promoting science and technology of MEXT and PRESTO to A.S. and the Swiss National Science Foundation (No. 31003A_125213) to H.A. We thank Haertel-Borer S. and R. Arlinghaus for many useful comments.

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