Genetic Management of Aquaculture-based Marine Stock Enhancement: Main Issues and Current Developments in Mississippi

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ABSTRACT

Stock enhancement is the release of cultured juveniles into the wild to augment the natural population and optimize harvests by overcoming recruitment limitation. A responsible and scientifically-based approach to stock enhancement was proposed by Blankenship and Leber [American Fisheries Society Symposia 15**:**167–175 (1995)] and includes the development and refining of production and stocking plans in conjunction with a thorough process of evaluation and monitoring of the success and impacts of programs. Management of genetic resources is an essential component of stock enhancement and aims to conserve genetic diversity and avoid deleterious genetic effects on wild stocks. Development of a genetic program to achieve those goals requires assessing and monitoring genetic diversity in the hatchery and in the wild populations being supplemented, understanding the structure of wild populations and local adaptation to develop adequate broodstocks to produce offspring for stocking, and also evaluating and mitigating possible impacts of the program on fitness. Here we review and discuss the main current issues related to the management of genetic resources during marine stock enhancement in the context of on-going enhancement efforts for Mississippi spotted seatrout (*Cynoscion nebulosus*).

KEY WORDS: Marine stock enhancement, marine aquaculture, genetic diversity, spotted seatrout, genetic management

Manejo Genético del Aumento de las Poblaciones Marinas a Través de la Acuicultura: Aspectos Principales y Desarrollos Actuales en Mississippi

El mejoramiento de los recursos pesqueros consiste en la liberacion en su habitat natural de juveniles cultivados con el fin de aumentar la poblacion natural y optimizar la cosecha pesquera contrarestando las limitaciones en reclutamiento. Blankenship y Leber [American Fisheries Society Symposia 15**:**167–175 (1995)] proponen con base en un enfoque cientifico y responsable el desarrollo de programas de mejoramiento de la reserva pesquera. Estos programas ademas de producir y liberar juveniles cultivados en habitat naturales buscan tambien su refinamiento con un monitoreo para determinar su eficacia e impacto. El manejo de los recursos geneticos es un componente escencial para el mejoramiento de las reservas pesqueras y se dirige a conservar la diversidad genetica evitando los efectos geneticos nocivos en los habitats naturales. El desarrollo de un programa genetico para alcanzar esos objetivos requiere crear un plan para evaluar y monitorear la diversidad genetica en los juveniles cultivados y en la poblacion natural que ha sido intervenida. Este plan aumentara el conocimiento en la estructura y adaptaciones locales de la poblacion natural y permitira tambien el seleccionamiento de reproductores adecuados para el mejoramiento de la reserva natural pesquera. Este plan permitira tambien evaluar y mitigar posibles impactos del programa sobre condicion fisica. En este estudio nosotros revisamos y discutimos los principales asuntos actuales relacionados con el manejo de recursos geneticos durante el programa de mejoramiento de corvinata pintada (*Cynoscion nebulosus*) en Mississippi.

PALABRAS CLAVE: Aumento de las poblaciones marinas, acuicultura, manejo genético, covinata pintada

Gestion Génétique des Programmes de Repeuplement pour les Espèces Marines: Principaux Problèmes et Développements Actuels dans le Mississippi

Le principe des programmes de repeuplement est de relâcher des juvéniles produits par l'aquaculture dans le milieu naturel pour augmenter l'abondance des populations et optimiser le volume des captures lorsque le recrutement est limité. Une approche responsable du repeuplement basée sur l'investigation scientifique a été proposée par Blankenship et Leber [American Fisheries Society Symposium 15**:**167–175 (1995)] et comprend le développent et l'optimisation de plans de production et de relâche en coordination avec une procédure approfondie d'évaluation et de suivi du succès et des impacts des programmes. La gestion des ressources génétiques est une composante essentielle du repeuplement et a pour objectif de préserver la diversité génétique et d'éviter les effets négatifs sur les populations naturelles. Le développement d'un programme génétique pour atteindre ces objectifs nécessite d'évaluer et de suivre la diversité génétique au niveau des écloseries et dans les populations naturelles soumises au repeuplement, déterminer la structure des populations et leurs adaptations génétiques aux conditions locales afin de développer des stock de reproducteurs appropriés pour la production des juvéniles qui sont relâchés, et enfin d'évaluer et d'atténuer les effets potentiels des programmes sur la fitness des populations. Nous faisons ici la revue critique des principales questions et problèmes lies à la gestion des ressources génétiques des programmes de repeuplement d'espèces marines dans le contexte du repeuplement de la spotted seatrout (*Cynoscion nebulosus*) dans l'état du Mississippi.

MOTS CLÉS: Programmes de repeuplement, espèces marines, gestion génétique, aquaculture

INTRODUCTION

Marine stock enhancement involves the culture and release of organisms into wild populations to augment the natural supply of juveniles and optimize harvests by overcoming recruitment limitation (Bell et al. 2008). Early attempts to develop stock enhancement programs date back to the 1900s when federal hatcheries were established on the United States Atlantic coast to produce and release eggs or yolk sac larvae of Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, Pollock *Pollachius virens*, winter flounder *Pleuronectes americanus* and Atlantic mackerel *Scomber scombrus* (Blankenship and Leber 1995). These programs were abandoned rapidly in large part due to the lack of technology to evaluate survival of the produced offspring and their contribution to recruitment of the targeted fisheries. Interest in stock enhancement re-emerged during the past couple of decades for multiple reasons. First an increasing number of fisheries stocks are declining due to overfishing and other anthropogenic impacts (Garcia and Newton 1997) and traditional management approaches are not always successful at rebuilding populations. In addition, the technology to spawn marine fishes in captivity, and rear their larvae and juveniles to a suitable size for release has become available for several species that could potentially benefit from stock enhancement. Also, major progress has been achieved in the technology for tagging and monitoring released offspring enabling evaluating results of programs.

Stock enhancement programs for marine fishes (not including anadromous species) are currently being developed on the U.S. West coast (California and Washington), in Hawaii, and in several states on the East Atlantic Coast and the Gulf of Mexico (Leber 2004). Potential benefits from marine stock enhancement are multiple and are outlined by Blankenship and Leber (1995). Implementation needs however to include evaluation and mitigation of potential negative impacts on supplemented populations. Accordingly, a responsible and scientifically based approach to stock enhancement was formulated by Blankenship and Leber (1995), recently updated by Lorenzen et al. (2010). The approach involves the development and refining of production and stocking plans in conjunction with a thorough process of evaluation and monitoring of the success and impacts of programs. Tasks to be undertaken under the responsible approach include the use of genetic resource management to maximize effectiveness of enhancement and avoid deleterious effects on wild populations.

Stock enhancement can impact genetic integrity of supplemented population in two main ways:
  i)   By reducing genetic diversity of the wild supplemented population thereby reducing the capacity of the population to evolve and adapt to environmental challenges, and
  ii) By directly disrupting local adaptation and fitness of the recipient population through the introduction of maladapted genes and genotypes.

The latter may occur if non-local brooders are used to produce offspring, but also if genetic change in the released population occurs due to differing selective pressures between the hatchery and wild environments. Below, we review the mechanisms of these sources of genetic impacts; the needs for evaluation and monitoring, potential management approaches for mitigation, and future research needs in the context of the on-going stock enhancement program for spotted seatrout in Mississippi.

THE MISSISSIPPI STOCK ENHANCEMENT PROGRAM FOR SPOTTED SEATROUT

The spotted seatrout (*Cynoscion nebulosus*) is a highly sought sciaenid fish in the northern Gulf of Mexico and is considered the most popular game fish in Mississippi coastal waters. The species is under close management in all Gulf states and Spawning Potential Ratios in Mississippi have been reported below traditional benchmarks for fisheries management (GSMFC 2001). A stock enhancement program was initiated in 2004 in conjunction between the University of Southern Mississippi Gulf Coast Research Laboratory and the Mississippi Department of Marine Resources. The programs aims to develop the methods to acquire, maintain, and spawn broodstock of spotted seatrout in order to facilitate production, rearing, tagging, releasing and assessing of juveniles. Techniques for intensive rearing of larvae and juveniles in closed recirculating systems have been developed in order to produce and release 5 - 6 inch spotted seatrout in Mississippi bays and estuaries. Fish are routinely tagged with Coded Wire tags before release to allow monitoring of returns. Separate broodstocks were established for the regions of Bay St Louis and Davis Bayou - Biloxi Bay; the two broodstocks are used to produce offspring that are released in those two bay systems respectively. Ninety thousands juveniles were released during the 2010 stocking season. Current objectives of the program include increasing production capability, assessment of the results of the program in terms of contribution of the offspring to recruitment, genetic monitoring, and optimization of culture and release methods. Genetic management was initiated in 2009 by developing a database of genotypes of broodfish spawned to produce released offspring and characterizing genetically spotted seatrout populations in Mississippi and neighboring states.

POPULATION STRUCTURE AND CHOICE OF THE ORIGIN OF BROODFISH FOR STOCK ENHANCEMENT

The choice of the origin of broodfish used to produce offspring to be released is of major importance when designing and establishing a stock enhancement program. Maintaining (multiple) separate broodstocks in order to stock distinct sub-populations of a species involves major costs and efforts and therefore, in several cases, one single broodstock is considered to stock broad geographic regions in the absence of reliable data on population structure. This leads to the potential issue of stocking fish of non-local genetic origin (i.e. produced from non-local brooders) if the population is subdivided within the geographic range covered by the program.

Potential Genetic Impacts if Non-local Fish Are Used as Broodstock

Introduction of fish of non-local genetic origin potentially induces genetic change in the recipient population if released and local fish interbreed. Such mixing can reduce the fitness of the recipient population due to a phenomenon referred to as outbreeding depression (Gharrett et al. 1999, Laikre et al. 2010), but can also lead to loss of genetic diversity at the species level to the long term if local genetic characteristics are removed due to repeated introgression by non-local genotypes, a phenomenon that has been referred to as genetic swamping (Allendorf and Luikart 2007, Roberts et al. 2010). Outbreeding depression can be due to the direct introduction of genes (alleles) that confer lower fitness in the local environment, but also to the breakdown of sets of co-adapted genes that were in linkage disequilibrium prior to supplementation in the local population and are recombined with non-local alleles in hybrids. If the supplemented population was locally adapted, these genetic changes are expected to reduce fitness. Another component of outbreeding depression is the reduced viability of hybrid offspring due to some form of hybrid dysfunction often translating in mortality at early life stages (Johnson et al. 2010). This second effect of outbreeding would be expected to impact directly recruitment in that energy allocated for reproduction by wild individuals would be 'wasted' in the production of hybrid with lower viability and fitness. This source of outbreeding depression seems to be a more moderate genetic risk for several marine species where low levels of divergence are commonly observed among geographic populations suggesting that gene flow and interbreeding occur naturally. Finally, repeated introduction of non-local genotypes ultimately can lead to loss of population structure and of unique regional genetic characteristics by promoting gene flow among historically isolated populations. While the extent of these negative consequences is still to be documented in marine species candidate for stock enhancement, determination of population genetic structure and identification of genetical-

ly divergent populations appears essential to the proper design of stocking programs.

Management Needs and Main Issues in Marine Species

Practical management of programs dealing with structured populations consists in using broodstock from identified population units to produce and release juveniles in geographic areas occupied by these populations. While this can be relatively easily implemented in freshwater and anadromous species where population structure is often well resolved, determination of population structure in marine species is particularly challenging because of the continuous nature of the habitat, large population sizes and high dispersal potential at larval and/or adult stages (Avise 1998). Interpretation of classical measures of divergence among populations is limited as homogeneity in allele distribution at neutral markers commonly used to infer population structure can be maintained even if populations exchange only a limited number of migrants each generation (Figure 1, Waples 1998). In that situation, demographically independent populations can exhibit apparent genetic homogeneity leading to the false inference of lack of subdivision (Gold et al. 2001). Another issue is that molecular markers used to infer population structure in most studies are presumably neutral to natural selection although variation at loci under selection is precisely the one that is important to determine occurrence of local adaptation and predict potential negative effects of outbreeding on fitness. For all these reasons, determination of population structure is still a forefront issue for management of stock enhancement. A precautionary approach that is usually taken consists in maintaining separate broodstocks for distinct hydrographic units such as bay systems for estuarine-dependent species, but these geographic subdivisions are often determined relatively arbitrarily rather than accounting for true genetic structure. This precautionary approach could potentially lead to the maintenance of large numbers of separate broodstocks for species distributed (and supplemented) over broad geographic areas leading to high associated costs and
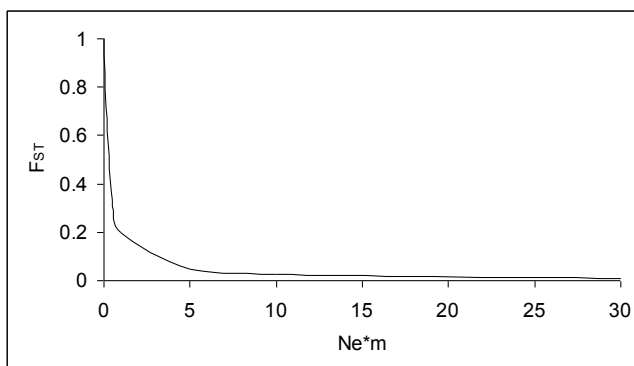

Figure 1. Expected values of F_{ST} assuming an island model of migration for a nuclear locus (based on equation 2)

challenging practical management of programs. Increasing efforts to understand population structure and determine appropriate management units seems therefore a priority for research.

Current Status and Prospects for Mississippi Spotted Seatrout

The life history features of spotted seatrout indicate a moderate potential for dispersal as compared to other long lived and/or more mobile sciaenids (Ramsey and Wakeman 1987). Adults have been reported to be sedentary during tag and recapture studies (Warren et al. 1998) with movement limited to a few kilometers for the majority of fish recovered. Dispersal could occur at early larval stages when eggs and larvae are pelagic. However spotted seatrout spawn relatively close to shore as opposed to other sciaenids such as red drum or Atlantic croaker, and therefore larval transport and dispersal may be more limited in this species. This limited potential for dispersal suggests that some degree of population structuring is not unexpected in spotted seatrout. Population genetic structure of spotted seatrout in the Gulf of Mexico was studied using allozymes, mitochondrial DNA and microsatellite markers. Studies were generally consistent with significant spatial structuring of populations in the southern U.S. waters according to an isolation by distance model (Gold et al. 1999 using mitochondrial DNA, Ward et al. 2007 using microsatellites markers, Ramsey and Wakeman 1987 using allozymes), although Wiley and Chapman (2003) also reported patterns of divergence among populations along the Atlantic coast that seemed related to zoogeographic barriers. The study conducted by Ward *et al.* (2007) was based on the most robust neutral dataset employed to date (8 microsatellites) and suggested that the genetic neighborhood size is relatively large (i.e. populations need to be distant by hundreds of miles to show detectable genetic differences). The allozyme studies provided interesting and contrasting results in that a clinal pattern of variation at the aspartate amino transferase 2 locus (AAT-2) was reported by King et al. (1993) along the Texas coast. The clinal distribution of allozyme variants seemed to follow a latitudinal axis possibly related to temperature and/or salinity regimes. These data suggest that selection and local adaptation may be a significant factor structuring spotted seatrout populations, despite the occurrence of gene flow suggested by the relatively low level of spatial divergence at microsatellites. We suggest that further assessment of population structure in the region should therefore include assessment of non-neutral genetic variation and local adaptation and their role in structuring spotted seatrout at the regional scale in the Northcentral Gulf of Mexico. This could be achieved by utilizing genomic approaches to search for regions of the genome impacted by natural selection. The characteristics of the habitats available for spotted seatrout change along an East-West axis from the low salinity waters of the

Mississippi sound to the higher salinity encountered in Alabama and West Florida coastal waters. Thus, in addition to the genomic approach mentioned above, assessment of the genetic basis of life history traits possibly involved in adaptation to local conditions (e.g. using common garden challenge experiments) would be beneficial. T hese approaches would enable evaluating possible negative effects of stocking non-local fish and also would allow documenting effects of environmental and anthropogenic pressures on fish populations including potential fisheries induced changes in life history traits.

ASSESSMENT AND MANAGEMENT OF EFFECTIVE POPULATION SIZE AND GENETIC DIVERSITY

Management and preservation of genetic diversity is a primary objective for the conservation of populations and species. Stock enhancement influences the breeding structure of supplemented populations and, in consequence, the genetic diversity that is being maintained in those population during and after stock enhancement.

Potential Impacts of Stock Enhancement on Genetic Diversity and Effective Population Size

Assessment and management of the effects of stock enhancement on genetic diversity of the supplemented populations requires an appropriate measure of genetic diversity. The population genetic parameter used to measure the genetic diversity that is maintained in a population is its effective populations size (N_e). Briefly, N_e is defined as the size of an ideal population that would experience the same amount of stochastic genetic change as the population under study. N_e thus determines the effects of finite population size on genetic variation and can be viewed as a standardized measure of the genetic diversity that is maintained in a population of interest. Different N_e parameters can be defined based on the different consequences of genetic drift exploited to derive estimates. The most widely used two N_e parameters are the variance N_e which is based on characterization of the temporal variance in allele frequencies at genetic loci and the inbreeding N_e which describes the rate of increase of probability of identity by descent (inbreeding) (Crow and Denniston 1988, Wang 1996). Consequences of supportive breeding on inbreeding N_e were highlighted in the work of Ryman and Laikre (1991) who established the relationship between the effective size of the wild and captive components of a population undergoing supplementation. The effects of supportive breeding on N_e can be described using the simple model that follows. One considers a wild population at an initial generation (t, Figure 1). A portion of the population is brought to the hatchery and spawned to produce offspring that are cultured and released as juveniles (generation t+1) and contribute a proportion x of the spawning population at generation t+2. The remaining portion of the population is left to spawn in the wild and

contributes a proportion 1-x to the breeding population at generation t+2 (Figure 2). Effects of the program are characterized by calculating the resulting overall N_e accounting for both the hatchery and wild components of the mixture spawning population at generation t+2. The overall resulting N_e is given by Equation 1 (Ryman and Laikre 1991):

$$\frac{1}{N_e} = \frac{x^2}{N_{eh}} + \frac{(1-x)^2}{N_{ew}}$$ Equation 1

Where N_e is the overall effective size of the mixed population, N_{eh} is the effective size of the hatchery population and N_{ew} the effective size of the wild (un-supplemented) population, x represent the proportion of fish of hatchery offspring contributing to the breeding population at generation t+2.

According to this equation, the size of the wild population is impacted by stock enhancement if (i) the contribution (x) of fish of hatchery descent is substantial and (ii) the effective size of the hatchery population N_{eh} is much smaller than that of the wild component N_{ew}. While condition (i) does not appear to be met yet in most marine programs, technical difficulties associated with maintaining large broodstocks of marine fishes usually does lead to very small captive spawning population as compared to the perceived size of the wild spawning stocks (i.e. (ii) is a likely situation in most current programs). Simulations presented in Figure 3 illustrate the reduction in N_e in a hypothetical scenario where the effective size of the captive fraction N_{eh} is 10 and various values for N_{ew} are considered for the wild component of the population (N_{ew} values correspond to the value of N_e when x = 0 for each curve in Figure 1). A sharp reduction of N_e (one order of magnitude or more) is predicted if the size of the wild population is large (> 10,000) for only moderate contributions of the program to the spawning population (less than 10% of the breeding population at generation t+2). Tringali et al. (1995) reviewed possible effects of marine stock enhancement on red drum populations based on estimates of the effective population size of the red drum wild population offshore the West Florida coast, and considering different hypothetical scenarios relative to the size of the captive spawning population and the contribution of fish of hatchery descent to spawning in the wild. Results indicated major reduction in effective size (leading to expected loss of genetic diversity) even for moderate contribution of the program to recruitment as illustrated in the example above.

Assessment and Management Needs and Issues in Marine Programs

The results above highlight the need to obtain baseline data on genetic diversity and effective size of the supplemented population and its natural rate of change before
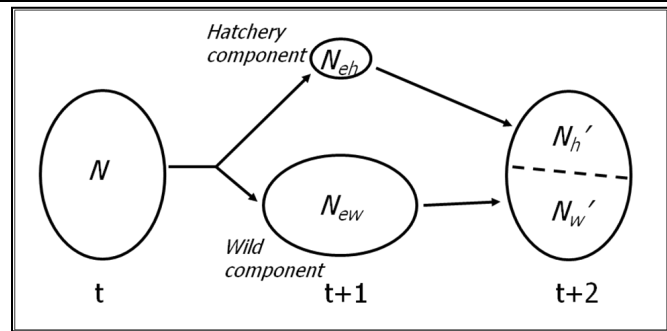

Figure 2. Schematic representation of aquaculture based stock enhancement. The total population produced at generation t is divided into a 'hatchery' component with effective size N_{eh} that reproduces in captivity and a 'wild' component of effective size N_{ew} that is left to reproduce in the wild. The N'_h and N'_w offspring of the two groups attempt to breed in the wild at generation $t + 2$. Adapted from Ryman et al. (1995).
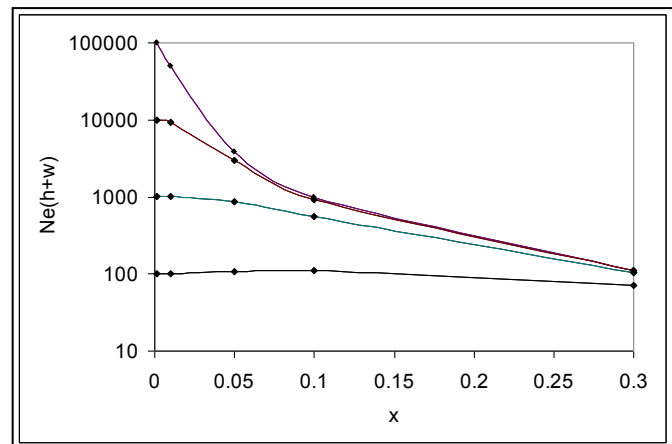

Figure 3. Total effective population size in a hypothetical case where a wild population is supported by a hatchery population with effective size Neh = 10. The x-axis is the proportion of offspring contributed by the captive parents. Individual curves correspond to different size of the wild population before supplementation (x = 0).

stock enhancement begins (Laikre et al. 2010). Further monitoring during and after supplementation is then necessary to detect and characterize changes in genetic diversity and effective size associated with stock enhancement. Characterization of the effective size of the hatchery breeding population used to produce offspring and the contribution of fish of hatchery descent (x) to spawning in the wild are also essential to quantify effects of the programs as highlighted above.

Assessment of the effective size of the captive population (N_{eh}) is often challenging considering difficulties in recapturing efficiently hatchery offspring at the time of spawning and measuring their reproductive success. An estimate of N_{eh} can be obtained by estimating the effective numbers of brooders contributing to offspring groups at the time of release and assuming that survival and reproduc-

tive success post release is randomly distributed (see e.g. Gold et al. 2008). Measurement of the contribution of hatchery offspring to spawning in the wild (x) can also be challenging because of the low probability of recapture of released fish reported in several many marine programs. Potential effects can however be evaluated considering various hypothetical scenario for x as above.

Current methods for assessment of the size of the wild population require knowledge of population structure in order to estimate N_e for subpopulations units usually assumed to display panmictia (Hare et al. 2011). When populations are partially connected to others, as is usually the case in marine species, explicit identification of populations sources of migrants to the target population is also needed for most methods. Considering the open nature of habitats used by marine populations, identification of population structure and sources of migrants can be particularly challenging as discussed above. For estuarine dependent species such as the red drum or spotted seatrout, N_e has been assessed considering bay systems as management units (Carson et al. 2009). Once population structure and management units are characterized, methods are available to estimate long term (historical) inbreeding N_e (e.g. Kuhner et al. 2006) or contemporaneous N_e via the temporal method (Waples 1989) or the linkage disequilibrium method (Waples 2006, 2008). The temporal method has been used extensively during the past few decades but can be seriously compromised if some of its assumptions are violated, in particular the absence of migration from other populations (Wang and Whitlock 2003). Estimates can be corrected accounting for migration from known source populations but the method remains to be evaluated in the case of large populations showing very low levels of divergence as is often the case in marine species. The linkage disequilibrium method has several advantages including the need for only one temporal sample, and relative robustness to a variety of demographic situations but it is unfortunately also limited in the case of large populations (Waples and Do 2010). In some cases, estimates of inbreeding N_e can serve as indicators of the effective population size prior to supplementation (Hare et al. 2011), and be used to set targets for conservation and stock enhancement. The combination of multiple approaches is usually recommended to increase reliability of inferences (Hare et al. 2011).

Another important question for the management of programs concerns the definition of target N_e values to be maintained in the supplemented population during stock enhancement. The minimum N_e that is required for a population to persist through evolutionary times has been the object of considerable investigations including population genetic viability simulations under various scenarios of environmental change (e.g. Gilpin and Soule 1986), determination of N_e needed to avoid accumulation of deleterious mutations (Higgins and Lynch 1995) or to avoid loss of genetic variation at quantitative traits (Bürger

and Lynch 1995). Minimum N_e values estimated using these approaches range between of 500 and 5,000; estimates from population viability analysis can even be larger if a long time frame is considered in simulations. The value of 500 has often been discussed as a minimum target largely based on the results of the above mentioned studies but, as pointed out by Waples et al. (2010), our understanding of the impacts of reductions of N_e for large populations is still very limited and caution may be exerted if the minimum effective size considered appears to be several orders of magnitude smaller than the estimated value of N_e prior to supplementation.

Management approaches to mitigate reduction in N_e resulting from stock enhancement programs involve essentially increasing the effective size and genetic diversity of released fish through increased broodstock size, frequent rotation to minimize contribution of individual fish, and avoidance of the use of fish of hatchery descent as brooders. The latter can be achieved through long term genetic monitoring and exclusion of fish of hatchery descent during broodstock replenishment based on parentage analysis.

Current Status and Prospects for Mississippi Spotted Seatrout

There is no information to date on the effective size of spotted seatrout populations in Mississippi or the effective size of groups of hatchery offspring being released. A first priority is therefore to generate these estimates by characterizing cohorts of wild and hatchery produced spotted seatrout using molecular markers and deploying the analytical approaches outlined above. Considering the recent initiation of the program and the relatively low number of hatchery produced fish that have been released to date, the obtained data on wild populations can serve as baseline information on population structure and levels of genetic diversity in supplemented populations, which will allow further monitoring as the program is being developed. Targets for N_e values in the hatchery can also be examined considering estimates for local wild populations and anticipated contribution of the hatchery program to recruitment as discussed above.

Selection at the Hatchery and Potential Effects on Fitness of Supplemented Populations

A third issue that has received particular attention during the past few years is the potential genetic change that could occur due to differing selective pressure between the hatchery and wild environments. Genetic change in supplemented populations can occur if natural selection is relaxed in the hatchery or if there is a positive selection favoring fitness in the hatchery environment (Araki et al. 2008).

Relaxed Selection in the Hatchery Environment and Positive Selection in the Hatchery

Relaxed selection in the hatchery environment is suggested by the survival rates reported during larval and juvenile phases in the hatchery as these survival rates are presumed to be higher than those in the natural environment. Accordingly, genotypes that would show reduced fitness and be removed from the pool of genotypes in the wild are not being removed in the hatchery. A possible outcome of this phenomenon is the increase in the frequency of deleterious alleles that were partially recessives in the wild population (Frankham 2008) or due to new mutations. This mechanism is unlikely to induce major genetic change unless mutation rates are extremely high and/or genomes are subjected to multiple consecutive generations of relaxed selection (Araki et al. 2008). The latter can easily be avoided in current programs where brooders are caught in the wild and the use of fish of hatchery descent can be prevented by pedigree analysis of candidate breeders brought to the hatchery for spawning.

Genetic change due to positive selection is expected to occur if the fitness of genotypes differs between the hatchery and wild environments. Negative impact on fitness of the wild population would be expected if higher fitness in the hatchery environment is correlated to lower fitness in the wild. The effect of this domestication selection is expected to be particularly important when domesticated strains are used as recently reported for Atlantic salmon (McGinnity et al. 2010). Current marine stock-enhancement programs usually involve spawning brooders caught in the wild and therefore domestication selection would be expected *a priori* to be minimal. However, some carry-over genetic effects on fitness were recently documented in a steelhead population (Araki *et al.* 2007) suggesting that captive rearing may impact fitness of wild populations even after a very limited domestication history.

Further study of the extent of genetic change induced by such differential selective pressures in the natural and captive environments and their impacts on fitness of supplemented populations seems warranted in marine species.

The potential for genetic change due to selection in the hatchery is determined primarily by the heritability of characters. Heritability is defined as the ratio of the additive genetic variance to the total phenotypic variance of a trait (Falconer and McKay 1996) and can be related to response of a population to selection through Equation 2.

$$R = h^2 \times S$$

Equation 2

Thus genetic change in response to selection is predicted to be a direct function of h^2 (traits with low h^2 will show little genetic change in response to selection) and the selection differential S where S is defined as the mean of selected parents minus the mean of the base population. Accordingly, evolution of a single trait in response to domestication selection is expected if the selective pressure is strong in the hatchery (i.e. S is large) and the heritability of the trait is high. As discussed by Araki et al. (2008), this situation is unlikely for single fitness traits. However, rapid evolution and fitness reduction may occur if selection in the hatchery acts on multiple traits at the same time and some of the traits are genetically correlated to fitness (Araki et al. 2008).

Assessment Approaches and Prospects for Mississippi Spotted Seatrout

Assessment of the effects of selection in the hatchery requires studying fitness of fish of hatchery and wild descent (see e.g. Araki et al. 2007). This will likely be difficult in several marine species because of the low probability of recapture in current programs and the need to evaluate the fitness of a large number of genotypes (families) of both wild and captive origins to achieve reliable assessment of differences in fitness attributable to domestication selection. A preliminary assessment of the effects of domestication can however be obtained by measuring heritability of survival during the hatchery phase and studying the architecture of traits impacting fitness in the captive environment.

Potential for selection or relaxed selection during hatchery rearing of spotted seatrout are still undocumented. Priorities for research thus include examining differential survival of genotypes during the hatchery phase and, to the longer term, comparing the fitness of offspring from fish of hatchery and wild descent.

CONCLUSION AND PERSPECTIVES

The potential genetic impacts of stock enhancement are multiple and their assessment and management is an essential component of the assessment and monitoring of marine programs. The spotted seatrout program in Mississippi began only a few years ago and releases to date have been moderate in numbers. The genetic monitoring plan that was recently initiated should therefore allow assessing genetic changes, if they occur, during the development of the program as the number of released fish scales-up to reach detectable contribution to the recruiting population. The sedentary life history of spotted seatrout likely makes this program a very good pilot project to document the genetic effects discussed above and their management.

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