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The importance of identifying spatial population structure in restocking and stock enhancement programmes

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Abstract

Most animal species show detectable genetic differentiation between populations, but the extent and pattern of this differentiation varies considerably between species. Some show gradual differentiation due to isolation by distance, some show chaotic patchiness, and some show relative uniformity over large distances with striking discontinuities over short distances. These varying patterns reflect both the dispersal powers of the organism and its population history. The evolution of locally adapted genotypes is facilitated in populations with restricted gene flow, and such co-adapted genotypes may then vary from population to population depending on local selective forces. Restocking and stock enhancement programmes need to be aware of the stock structure of the target species, as the introduction of genotypes unrepresentative of the augmented population can have negative effects. Swamping the native population with large numbers of genotypes from a few matings, even if derived from the native population, can also be detrimental. It follows that, wherever possible, restocking and stock enhancement programmes should use broodstock taken directly from the population to be enhanced, and that large numbers of broodstock should be used. If broodstock cannot be taken from the population to be enhanced, they should be taken from the genetically most similar population available. Restocking and stock enhancement programmes should be genetically monitored to determine their impacts and outcomes.

Keywords: Outbreeding depression; Inbreeding depression; Hybrid vigor; Broodstock numbers; Genetic population structure

1. Introduction

Stocks of many species of fish and shellfish have become depleted through factors such as over-fishing and habitat degradation. Most marine stocks are either over-fished or fully exploited, with only a small minority under-exploited (Fig. 1). Fisheries could, in the long-term, be improved by better management, by reducing fishing effort and by restoring habitat where possible—however, none of these options is easy in practice. Another possible option, for selected fisheries, is to release hatchery-reared juveniles into the wild. This has been widely practised for salmonid fisheries in the USA and, in Japan, some 90 species of fish and invertebrates have been released to augment wild stocks (Honma, 1993; Imamura, 1999). The pros and cons of this approach have been widely debated (e.g., Blankenship and Leber, 1995; Munro and Bell, 1997; Hilborn, 1998; Travis et al., 1998; Blaxter, 2000; Caddy and Defeo, 2003; Leber, 2004; Lorenzen, 2005).

Release of cultured juveniles into the wild may either be for restocking – the restoration of spawning biomass for a severely depleted non-operational fishery enabling a sustainable fishery to be re-established, for enhancement – the augmentation of an existing fishery to enable larger catches to be taken, or for creating new fisheries (Blankenship and Leber, 1995; Cowx, 1998; Welcomme and Bartley, 1998; Leber et al., 2004; Bell et al., 2005).

Natural selection operating on the genetic variation present in wild populations will select for particular genotypes and gene complexes that maximise fitness of individuals in a specific environment. Co-adapted genotypes will arise, and these genotypes are likely to differ from population to population depending on local selective forces. Restriction of gene flow between populations will promote the adaptive divergence of different populations.

Local adaptation means that introduced fish from a genetically divergent population of the same species are generally expected to be less fit in the recipient population than native

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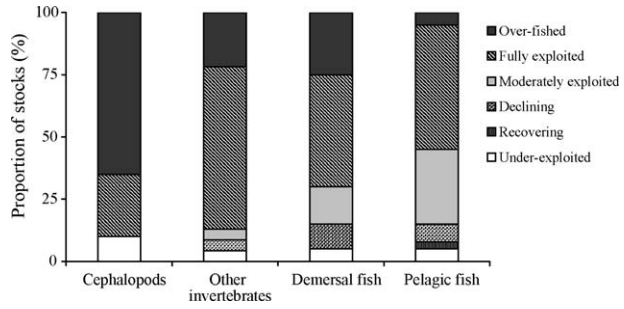

Fig. 1. The proportion of marine stocks ranging from under-exploited to over-fished for four categories of marine fisheries (redrawn from Hall, 1999).

fish, and that if the introduced fish breed with native fish, then the new hybrid population is expected to be less fit than the original native population (e.g., Hindar et al., 1991; Philipp et al., 2002). This latter effect is termed outbreeding depression. Simulations show that it increases linearly with genetic distance between populations (Edmands and Timmerman, 2003). A loss of fitness might also result if the local population is swamped with large numbers of closely related genotypes derived from a small number of broodstock (Ryman and Laikre, 1991). This is a form of inbreeding depression.

However, sometimes newly introduced genotypes might hybridise with pre-existing genotypes of that species in a positive way, leading to hybrid vigor in the F1 generation. Such hybrid vigor is likely to reduce in subsequent generations (Falconer and Mackay, 1996).

This paper briefly describes the different patterns of genetic population structures that occur for fish and shellfish, and gives some examples. It then discusses the possible genetic effects of introductions, again with examples. Genotype introductions from genetically similar populations are likely to have smaller negative effects than the introductions from genetically dissimilar populations. Therefore, it is necessary to have a good understanding of population structure before carrying out any restocking or stock enhancement project (Cross, 2000). This can often be achieved by molecular genetic analysis, supplemented where necessary with data from other sources (such as tag results, analysis of parasite loads, otolith microchemical examination). This review does not consider the impacts of transgenic fish and the effects of transplants into areas outside the native range of the species.

2. Identification of the genetic structure of populations

2.1. Methodology

Genetic diversity within and between populations can be examined by either DNA or protein-based methods. The pros and cons of the various approaches have been widely discussed (e.g., Ryman and Utter, 1987; Ward, 2002; Beaumont and Hoare, 2003). Once individual locus genotypes (or haplotypes in the case of mitochondrial DNA) have been identified, within and between population diversity can be quantified. Nuclear genome diversity can be examined for fits to Hardy–Weinberg expectations (the expected distribution of genotype frequencies under the assumption of random mating). Deviations from Hardy–Weinberg equilibrium might reflect non-random mating, population mixing, natural selection, or incorrect identification of genotypes.

The extent of genetic differentiation between samples or populations can be quantified through the use of F_{ST} or analogous statistics (Wright, 1969). An F_{ST} value of 0.06 (for example) means that 6% of the detected variation arises from inter-population differences and 94% from intra-population differentiation. Hierarchical analyses may also be carried out by assigning all subpopulations in a particular group to that group, and estimating levels of divergence not just across all subpopulations but also between groups. F_{ST} values have also been used to estimate numbers of migrants among populations ($N_e m$, where N_e is the effective population size and m is the migration rate), through the relationship $F_{ST} = 1/(1 + 4N_e m)$ (Wright, 1969). Low F_{ST} values equate to high numbers of migrants. However, there are many problems with doing this (Bossart and Prowell, 1998; Waples, 1998; Whitlock and McCauley, 1999), and any such derived estimates are likely to be, at best, crude approximations. For example, $N_e m$ values increase dramatically as F_{ST} values fall below about 0.02 (see Fig. 2), and so any error in a low F_{ST} estimate equates to a huge error in $N_e m$. Furthermore, the relationship is only true under certain conditions, which include an island model of migration and population equilibrium between mutation and drift.

Several other ways of examining genetic population relationships have recently been proposed. These include nested clade analysis based on evolutionary relationships among alleles or haplotypes and their spatial frequencies (Templeton, 1998), and coalescence genealogy-based methods for estimating migration rates and effective population

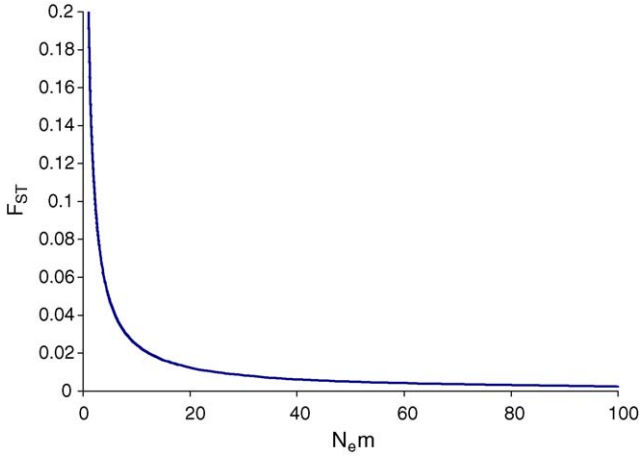

Fig. 2. Relationship between $N_e m$ (numbers of migrants) and F_{ST}, based on the equation $F_{ST} = 1/(1 + 4N_e m)$ (Wright, 1969).