Genetic principles for freshwater restoration in New Zealand

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Abstract   Habitat fragmentation and destruction can lead to loss of genetic diversity within and among populations. One goal of restoration projects is to minimise loss of genetic diversity and to preserve genetic structure. Restoration may involve the release of wild-caught or hatchery-produced individuals to re-establish or augment populations, and targets species with weak dispersal potential. Key criteria to consider in restoration projects are genetic divergence among the source populations and the number of individuals to transfer. Molecular tools provide quick and simple tools for assessing genetic diversity, but most markers are selectively neutral and should be supplemented with data on life-history traits. The effective size of the population, N_e, can be considerably smaller than the census N. Low numbers of founders will lead to a loss of genetic diversity, whereas subsequent breeding between closely related individuals will lead to inbreeding depression. Outbreeding depression can occur when offspring are produced from crosses between individuals from divergent populations, leading to the breakdown of co-adapted gene complexes. Both inbreeding and outbreeding depression can lead to declines in fitness, and these effects may take several generations to become evident.

Keywords   effective population size; outbreeding and inbreeding depression; genetic restoration

INTRODUCTION

Restoration of biota, the augmentation or re-establishment of extirpated populations or communities, is becoming increasingly common as freshwater populations are reduced through habitat loss and degradation, species introductions, and overfishing (e.g., Clewell & Aronson 2007). Restoration typically involves the supplementation of populations with translocated stock or seed from wild populations or from hatcheries (Ryman 1991; Falk et al. 2006). Although the focus of restoration projects has been necessarily ecological (Anon. 2004a; Clewell & Aronson 2007; Katz et al. 2007), some genetic impacts are inevitable if novel genes or genotypes are inadvertently introduced from foreign source populations (McKay et al. 2005). The general genetic principles of restoration have been considered (McKay et al. 2005; Falk et al. 2006) and specifically reviewed for key freshwater species in Australia (Hughes 2007). Restoration genetics is a relatively new branch of conservation genetics (Tallmon et al. 2004; Hedrick 2005; McKay et al. 2005; Falk et al. 2006), which draws on genetics theory and its applications to small populations (Soule 1988; Nunney & Campell 1993). Genetic principles have been applied in plant restoration projects (McKay et al. 2005; Ramp et al. 2006; Takagawa et al. 2006) and widely considered in the restoration of commercial fish populations, notably salmonids (Ryman 1991; Utter 2004; Verspoor et al. 2007). Genetic guidelines have been developed for the restoration and enhancement of commercially important shellfish (Munro 1993; Benzie & Williams 1996; Gaffney 2006) and fish stocks (FAO 1993; ICES 1996). Increasingly, genetic data are being considered in restoration projects of other non-salmonid freshwater fishes and invertebrates (Vrijenhoek 1998; Sheller et al. 2006; Cook et al. 2007; Demand & Bjorklund 2007; Hughes 2007).

The success and timescale of re-colonisation will be driven by dispersal potentials of the organisms, which range from strong dispersers such as migratory fishes and winged insects to weak dispersers such as crustaceans (Malmqvist 2002; Hughes 2007).

Even sessile species such as mussels may be able to disperse over tens to hundreds of kilometres through the juvenile stages which are obligate parasites on fishes (e.g., Elderkin et al. 2007). Restoration projects that depend on natural re-colonisation (passive restoration) of organisms need to ensure that restoration sites and habitat connectivity networks are established at appropriate scales to promote re-colonisation. Restoration projects targeting weak dispersers need to consider translocation of key organisms. Successful reintroduction of populations to restored habitats will be dependent upon a wide range of ecological and demographic factors for which an understanding of genetic differentiation among potential source populations is desirable (Falk et al. 2006).

In New Zealand there are many local and national initiatives in freshwater restoration (see for example: www.nzfreshwater.org/home.html; www.lernz. co.nz/; www.sustain.canterbury.ac.nz/waterways/ resources.shtml). Specific studies have considered restoration of fishes (Richardson & Jowett 2005; Jowett et al. 2009, this issue; Leathwick et al. 2009, this issue), invertebrates (Blakely et al. 2006; Winterbourn et al. 2007), and lake macrophytes (de Winton et al. 2000); whereas species recovery plans have been developed for the threatened non-diadromous mudfishes (Eldon 1993; Anon. 2003) and galaxiid fishes (Anon. 2004b). Here the genetic principles of restoration are considered with a focus on weak dispersers that are unlikely to establish populations in restored habitats over ecological timescales of a few generations. Although restoration genetics is intimately entwined with ecology and life-history traits, the key genetics questions can be distilled into two areas: selection of appropriate source populations and the numbers of individuals to transfer.

Genetic goals of restoration

Genetic goals of restoration projects are not always explicitly stated but share those of conservation genetics, to preserve evolutionary processes and the ecological viability of populations (Moritz 1994; Waples 1995; Falk et al. 2006), and specifically to maintain genetic resources without avoidable and irreversible loss of genetic diversity during the restoration process (Ryman 1991). However, the focus of conservation genetics is on rare and endangered species and differs subtly from restoration genetics, which may target species that are common outside the restoration area. One goal of conservation genetics is to restore or increase genetic diversity within

small fragmented populations through translocation (Frankham et al. 2004; Allendorf & Luikart 2006), whereas a translocation goal of restoration projects is to avoid loss of genetic diversity in the restored population (Ryman 1991; Falk et al. 2006). In the absence of information on the ecological and evolutionary value of most genes or populations, the main focus of restoration projects has been aimed at maintaining genetic diversity within and between populations (Ryman 1991). Retention of genetic diversity has been an important component in the restoration and stocking programmes developed for freshwater Salmonidae (Utter 2004; Page et al. 2005) and Percidae (Wilson et al. 2007) in North America. To maintain genetic resources and minimise the risk of loss of genetic diversity, the source populations should be genetically close to those of the restored populations; and it is generally recognised that it is prudent to avoid the transfer of individuals among genetically discrete units (Moritz 1994). Consequently, a primary goal of freshwater restoration genetics is to define population genetic structure (Vrijenhoek 1998; Hurwood et al. 2003; Hogg et al. 2006; Hughes 2007). The second, main goal is to ensure that restored populations persist over time (Falk et al. 2006) and this goal requires that sufficient numbers of founders are established, and, if necessary, supplemented with additional introductions.

Genetic diversity and identification of source populations for restoration

There is a considerable literature that discusses and defines conservation units below the species level. Ryder (1986) first proposed the term Evolutionary Significant Unit (ESU) (Box 1), which has been widely applied and re-defined in conservation biology, although the differences lie more in the criteria used to define ESUs than in their fundamental essence (Fraser & Bernatchez 2001; De Guia & Saitoh 2007). Guia & Saitoh (2007) introduced the terms partial and full ESUs to recognise situations where partial ESUs were defined on the basis of one aspect (e.g., molecular based ESU), and full ESUs based on information derived from both neutral and adaptive genetic variation. Moritz (1994) used the term management unit (MU) (Box 1), which concerns current population structure, and is broadly equivalent to the stock concept used in fisheries management. The terms conservation unit (CU), and operational conservation unit have been used at a more pragmatic level to refer to either ESUs , MUs, or geographical units that managers

consider important to conserve (Manel et al. 2003; Johnson & Belk 2007). Population is widely used in the ecological and evolutionary literature, and in a review of population definitions, Waples & Gaggiotti (2006) pointed out that although there is no consensus over a quantitative definition of a population, there are two main definitions that reflect ecological and evolutionary paradigms (Box 1).

In practice, the identification of MUs, CUs, and evolutionary populations has been dominated by the application of molecular tools (Box 2), because of the relative ease with which genetic data can be collected. Restoration projects may not have sufficient time or resources to establish ESUs, and there is a risk that identification of MUs and CUs based on one type of data (particularly neutral genetic markers) may overlook genetic population differentiation. For example, a laboratory study of genetic variation in *Drosophila* showed no relationship between the levels of variation with molecular markers and life-history characters (Lynch et al. 1999). Adaptive divergence may occur rapidly through accumulation of genetic differences driven by local selection (Lynch 1996; Reznick et al. 1997; Bell 2001; Binks et al. 2007). Rapid changes in allozyme (Box 2) frequencies occurred in large mouth bass *Micropterus salmoides* exposed to warm water effluent from power stations (Smith et al. 1983), and rapid changes in allozyme frequencies and shell shape were reported for translocated populations of the marine intertidal snail *Bembicium vittatum* (Binks et al. 2007). New molecular techniques may allow the detection of adaptive variation by examining functional genes (Schöffmann et al. 2007), as applied in the identification of populations in marine fishes (Pogson & Mesa 2004; Larsen 2007). Genes under selection, or associated with markers under selection, are expected to show higher population divergence than neutral markers, in particular for organisms with large population sizes, where selection will be a more powerful force than genetic drift (Endler 1986).

Genetic diversity in freshwater fishes and invertebrates

Freshwater species in general show greater population divergence (i.e., more MUs) than marine or terrestrial species, owing to the greater number of barriers to dispersal and migration (Gyllenstein 1985). The most widely used measure of genetic differentiation between populations is G_{ST}, or its analogue Φ_{ST} that takes into account haplotype and sequence divergence (Nei 1973, 1987). G_{ST} is a relative measure ranging between 0 (identical

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Box 1 Populations and conservation units below the species level.

Evolutionary Significant Unit (ESU)
- Populations possessing genetic attributes significant for present and future generations (Ryder 1986).
- Reciprocally monophyletic for mitochondrial (mt)DNA alleles and show significant divergence of allele frequencies at nuclear loci (Moritz 1994).
- A lineage demonstrating highly restricted gene flow from other such lineages within the higher organisational level of the species (Fraser & Bernatchez 2001).

Management Unit (MU)
- Populations with significant divergence of allele frequencies at nuclear or mitochondrial loci regardless of the phylogenetic distinctiveness of the alleles (Moritz 1994).

Conservation Unit (CU) and Operational Conservation Unit (OCU)
- A population or group of populations important to be conserved (Manel et al. 2003; Geist & Kuehn 2005a,b; Araguas et al. 2007).
- Continuous area limited by geographical boundaries, and inhabited by one or more populations sharing the same genetic pattern (Araguas et al. 2007).

Evolutionary population
- A group of individuals of the same species living in close enough proximity that any member of the group can potentially mate with any other member (Waples & Gaggiotti 2006).

Ecological population
- A group of individuals of the same species that co-occur in space and time and have an opportunity to interact with each other (Waples & Gaggiotti 2006).

allele frequencies in the populations) and 1 (different alleles fixed at each locus). Genetic differentiation, measured with allozyme markers, was inversely related to dispersal ability across 333 species of vertebrates and invertebrates from terrestrial, marine, and freshwater environments (Bohonak 1999). A review of the literature on allozymes (see Box 2) showed that the mean G_{ST} for marine fishes was 0.06,

for anadromous species 0.11, and for freshwater fishes 0.22 (Ward et al. 1994). It should be noted that marine fish tend to have higher heterozygosities and more alleles than anadromous species, which in turn are more variable than freshwater fishes measured with both allozyme (Gyllenstein 1985; Ward et al. 1994) and microsatellite markers (Dewoody & Avise 2000), owing to the larger evolutionary effective

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Box 2   Molecular tools for estimating genetic diversity in natural populations.

Molecular biology has provided a range of tools for measuring genetic variation in natural populations. Most markers have been assumed to be selectively neutral, and statistical tests are available to detect natural selection in patterns of genetic variation (Ford 2002).

Polymerase chain reaction (PCR)
PCR revolutionised molecular genetic studies, by enabling specific segments of DNA to be amplified to provide millions of copies, which can be visualised or further manipulated to analyse genetic variation. Amplification of DNA allows genetic analyses from non-lethally collected tissue samples.

Allozymes
Allozyme loci are protein coding genes. Genetic variation is detected indirectly, through changes in the overall charge on the protein molecule, and migration through a gel (gel electrophoresis), but can be underestimated because changes that do not result in a charge difference are not detected. The technique was widely used for 30 years in population-genetic studies, but has been largely replaced by tools that measure genetic variation directly at the DNA level.

Microsatellite DNA
Microsatellites are highly variable regions of DNA. They are characterised by short segments of DNA that contain a repeated sequence of 1–5 basepairs (bp), such as $(CTA)_4$. Microsatellites are widely dispersed along the chromosomes, with no known coding functions (unlike genes which code for specific proteins). The lack of coding constraints ensures that mutations accumulate more quickly than in coding regions of the DNA.

In fishes, allozyme loci typically have 2–3 alleles, occasionally up to 10 alleles per locus, with heterozygosities ranging from 0 to 18%; microsatellite loci have 5–30 alleles, sometimes more than 50, with heterozygosities >70% (Dewoody & Avise 2000). The very high level of genetic diversity can present problems for analysis and biological interpretation of microsatellite data sets (Hedrick 1999).

Mitochondrial DNA
Mitochondrial (mt)DNA is the small genome found within the mitochondria. In vertebrates and most invertebrates mitochondria are passed from mother to offspring in the egg. The haploid genome, with lack of recombination, reduces the N_e (effective population size) of mtDNA to ¼ of that for nuclear DNA, increasing the potential for genetic drift among populations. There are several approaches to analysis, from fragmentation of the overall mtDNA genome with restriction enzymes (restriction fragment length polymorphisms = RFLPs) through to direct sequencing. Some regions of the mitochondrial region are non-coding and often highly variable (the control region) and used for population studies, while the less variable coding regions are used for phylogenetic studies.

Nuclear-encoded ribosomal RNA genes
Ribosomal RNA genes are among the most abundant elements of DNA in the cell and exist as repeat units separated by the internal transcribed spacers (ITS). The conserved 18S and 28S ribosomal sequences have been used in phylogenetic studies, whereas the less conserved ITS regions have been used to study closely related species.

Several other nuclear DNA tools are available, such as the multilocus RAPDs, random amplified polymorphic DNA (Kliber & Eckert 2005) were quickly surpassed; others such as introns, non-coding regions of nDNA (Belshaw & Bensasson 2006); SNPs, single nucleotide polymorphisms; MHC, major histocompatiblity complexes; and AFLPs amplified fragment length polymorphisms (Bensch & Akesson 2005), have not been widely applied in population studies of freshwater organisms to date, other than Salmonidae (Langefores et al. 1998; Vasemagi et al. 2005; Dionne et al. 2007; Hansen et al. 2007; Rogers et al. 2007).

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population sizes in marine fishes (Dewoody & Avise 2000).

Comparisons of genetic diversity in Australian freshwater species have shown winged insects were the most extensive dispersers across catchment boundaries whereas non-diadromous fish and insects were good dispersers within catchments, although fish dispersal was limited to species in lowland streams (Hughes 2007). It was concluded that with the exception of fish in lowland streams and insects, natural re-colonisation of restored sites was only likely to occur from within the same stream (Hughes 2007).

There are limitations in using selectively neutral molecular markers to estimate genetic divergences, because these tools measure divergence at evolutionary and not ecological timescales. Where there is significant genetic differentiation among populations/sites, then differentiation can be used to infer lack of gene flow. The converse, lack of genetic differentiation among sites, may not be owing to current gene flow, and needs to be considered in parallel with ecological and life-history data. Lack of genetic differentiation among populations of winged insects in neighbouring catchments might reflect pre-fragmentation connectivity rather than present day gene-flow via adult flight (Monaghan et al. 2001; Finn & Adler 2006; Smith et al. 2006a). Extensive de-forestation over the past 200 years may have created barriers to dispersal and extirpated populations in lowland catchments, where dispersal among populations may have been less constrained by geography than among populations in the hill country (Hughes 2007).

Minimum numbers for active genetic restoration

Genetic variation allows populations and species to persist through changing environments over evolutionary timescales, and is determined by the combined effects of mutation, random genetic drift, selection, and gene flow (Box 3). Mutations are the ultimate source of genetic variation, but are rare and not important over the timescale of restoration projects. Restored populations based on small numbers of founders with low genetic variation may risk extinction long after population size has recovered, because genetic variation is only restored through accumulation from mutations over numerous generations or through gene-flow (Lynch et al. 1999). Population genetic theory shows that a minimum effective population size, N_e (Box 3) of 50, with an equal sex ratio, is required to retain 99% of genetic

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Box 3 Genetic processes in natural populations.

Genetic drift and N_e (effective population size)
The genetic composition of a population can change over generations owing to chance events, which are most relevant in small populations. Alleles (genetic variants) may become fixed or lost from small populations regardless of their adaptive value. The effective size of the population, N_e (Wright 1951)—a measure of the number of individuals contributing to the next generation—can be considerably smaller than the census population (N) owing to variations in population size between generations, reducing the effective population size to the harmonic mean over generations (Wright 1940). Unequal sex ratios and random variations in reproductive success further reduce N_e.

Selection
Selection is the differential reproductive success of genotypes. Under natural selection, the more fit individuals leave more offspring than less fit individuals, leading to adaptive change in populations. Selection may act at one or a few loci whereas genetic drift and gene flow act on all loci. Specific genotypes can have different selective values under different environmental conditions leading to balanced polymorphisms. Evidence for natural selection in fish populations is limited to a few well researched cases for qualitative (Mitton 1997) and quantitative markers (Reznick et al. 1997), and can be rapid (Smith et al. 1983; Stockwell & Weeks 1999; Bell 2001).

Gene flow, migration, and dispersal
Gene flow is the movement of genes and their establishment in neighbouring populations and counteracts the effects of drift and selection by introducing new alleles into populations. In two populations of size N, which exchange a proportion m through immigrants at each generation, substantial differentiation (at neutral loci) will not occur when $Nm > 1$ (Slatkin 1987). Because N is large in many wild populations, a small absolute number of immigrants at each generation will prevent populations from diverging owing to drift. Migration is the long-distance movement of large numbers of individuals, in the same general direction at the same time, and includes the seasonal movement between feeding and breeding areas, whereas dispersal is the random movement of individuals between localities (Endler 1977; Bilton 2001)). For salmon, migration includes the return of adults to their natal site (= homing). Mark-recapture studies provide an indication of dispersal and migration, but not a measure of reproductive success and gene flow.

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variation per generation. Experimental studies with the housefly *Musca domestica* have shown that N_e >50 is necessary for populations to retain fitness and escape extinction, even in the short term (Reed & Bryant 2000). A minimum N_e of 500 has been suggested for the long-term preservation of genetic diversity (Franklin 1980; FAO 1981; Soule 1988) and N_e of 5000 to retain evolutionary potential in natural populations (Lande 1995). Unequal sex ratios and variations in reproductive success reduce N_e and can result in N_e several orders of magnitude smaller than census size (Frankham 1995a). Estimates of N_e/N average 0.1 in 102 species (Frankham 1995a), and in insects range from <0.0001 to 1 (Frankham 1995a) and in fishes from 0.01 to 1 (Frankham 1995a; Miller & Kapuscinski 1997; Hedrick et al. 2000).

Small effective population size will result in a loss of rare alleles in the founding population, and lead to a risk of inbreeding in subsequent generations (Lynch 2005). The rate of inbreeding is given by: $\Delta F = 1/(2 N_e)$, where ΔF is the rate of inbreeding per generation and N_e is the effective population size. Inbreeding is cumulative because it increases from one generation to the next. Inbreeding depression is the reduced fitness in a population as a result of breeding between related individuals (Lynch 2005). Inbreeding depression is difficult to demonstrate in wild populations and is more commonly observed in domesticated animals and laboratory populations as lower survival or reproductive rates (Visscher et al. 2001). Although inbreeding is unlikely in many wild populations, it could occur when populations have been severely reduced in size and are supplemented with hatchery or translocated stock derived from a few parents (Bartley et al. 1992; Hedrick et al. 1995). Inbreeding in small populations (N <1000) may be more important than chance variations in survival and reproduction, and has contributed to the decline and extinction of several rare mammals and birds (Frankham 1995b). Yet, some vertebrate populations have survived despite severe reductions in population size (N < 100) e.g., elephant seals (*Mirounga angustirostrus*) (Bonnell & Selander 1974), European bison (*Bison bison*) (Lacy 1997), and park cattle (*Bos taurus*) (Visscher et al. 2001).

One scenario to avoid inbreeding would be to use outbreeding enhancement by transferring stock from different populations to establish the restored population. This form of line crossing is used by plant and animal breeders to gain hybrid vigor, but the increase in productivity traits obtained in the first generation can be followed by outbreeding depression in subsequent generations (Lynch 2005).

Outbreeding depression appears when offspring from crosses between individuals from different populations have lower fitness than progeny from crosses between individuals in the same population, and a result of the breakdown of coadapted gene complexes that have evolved in divergent populations (Lynch 2005). Outbreeding depression might also occur through the swamping of locally adapted genes when large numbers of individuals are introduced into small populations, as has occurred in some salmon populations (Hindar et al. 1991; Ryman 1991; Bartley et al. 1992; Ayllon et al. 2006). Swamping displaces the adaptive gene complexes through the introduction of genes that are adapted to the hatchery environment or to some other locality.

Theoretical and empirical studies show that both inbreeding depression and outbreeding depression can lead to the decline in fitness of populations, and both effects may take several generations to become apparent. Thus prevention may be a better restoration option than waiting several generations before attempting corrective actions (Lynch 2005; Takagawa et al. 2006).

Although N_e can be used to guide the minimum number of founders to establish a restored population, consideration has to be given to persistence over many generations. Population size is a major determinant of extinction risk and populations with N_e <100 and N <1000 are highly vulnerable to extinction (Lynch et al. 1995), but there is controversy as to how large populations need to be to ensure persistence. The minimum viable population (MVP) describes the smallest size at which a population or species can exist without facing extinction from natural disasters or demographic and genetic stochasticity (Reed et al. 2003). The size of MVPs are highly specific and dependent on the environmental and life-history characteristics of the species. MVPs have been simulated with population viability analyses (PVA), which provide a quantitative means for predicting the probability of extinction, by using population-specific life-history information to forecast future population sizes, and take into account the combined impacts of stochastic (demographic, environmental, and genetic) and deterministic factors such as habitat loss and over-exploitation (Reed et al. 2003). The mean and median estimates of MVPs in 102 vertebrate (mostly terrestrial) species, with a 99% probability of persistence over 40 generations, were 7316 and 5816 adults, respectively (Reed et al. 2003), leading the authors to conclude that the lack of long-term studies for many endangered species has led to widespread underestimations of extinction risk.

Census numbers are not known for most of the non-diadromous fishes in New Zealand, but the new species of *Galaxias* fishes recently described from South Island, New Zealand have restricted distributions and presumed small population sizes (McDowall & Waters 2002, 2003) and are recognised as threatened or data poor (Anon. 2004b). The longjaw galaxid *Galaxias cobitinis* is restricted to the Kakanui and Waitaki catchments in the eastern South Island (McDowall & Waters 2002) with an estimated adult population of N <250 individuals in the Kauru River (Kakanui catchment), and is recognised as Nationally Critical (Anon. 2004b).

ESUs and MUs in New Zealand freshwater species

The key freshwater taxa likely to be considered in restoration projects in New Zealand are the non-diadromous fishes (*Galaxias*, *Neochanna*, and *Gobiomorphus*), molluscs (*Echyridella*), crustaceans (*Paranephrops* and *Paracalliope*), insects, in particular the EPT taxa, Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies), and lake macrophytes. An initially unexpected but recurring finding in molecular studies has been the number of potentially cryptic species in fishes (Allibone et al. 1996; Gleeson et al. 1999; Ling et al. 2001; Waters & Wallis 2001; Smith et al. 2005), crustaceans (Hogg et al. 2006; Apte et al. 2007), and insects (Hogg et al. 2002), many of which have restricted distributions and small population sizes, making them vulnerable to land use changes and introduced predators. Ecological aspects of restoration of insects and fishes are discussed in other papers in this issue (Jowett et al. 2009; Leathwick et al. 2009) and in other reports for fishes (Anon. 2003, 2004b; Richardson & Jowett 2005). The requirements for captive breeding of mudfish *Neochanna* have been considered by Dunn & O'Brien (2005).

Extensive habitat loss and degradation along with wetland drainage and de-forestation over the past 200 years may have created barriers to dispersal and extirpated populations, particularly in lowland catchments where populations were less constrained by landscape than in the hill country. Species of mudfish *Neochanna* are threatened (Anon. 2003) as are many of the non-diadromous *Galaxias* (Anon. 2004b). Although many EPT taxa are not considered threatened, the recently isolated populations may be vulnerable to further de-forestation activities that reduce connectivity pathways and population sizes, because small effective populations are likely to retain lower levels of genetic diversity (Lynch et al. 1995; Allendorf & Luikart 2006). Present day populations of winged insects (EPT) may have been isolated over ecological as opposed to evolutionary timescales, and have had insufficient time to reach an equilibrium between gene flow (that restricts divergence) and drift (that enhances divergence) among populations. Even comparatively small environmental changes such as the placement of road culverts could act as partial barriers to upstream flight patterns of insects (Blakely et al. 2006), and consequently restrict adult dispersal and gene-flow.

Genetic diversity in New Zealand freshwater fishes

New Zealand was long regarded as having a depauperate fish fauna (Ling et al. 2001) but molecular studies over the past decade have revealed a species flock, the *G. vulgaris* complex, in the South Island (Allibone et al. 1996; Waters & Wallis 2001), cryptic species of mudfish *Neochanna* (Gleeson et al. 1999; Ling et al. 2001), and high sequence divergence in the upland bully *Gobiomorphus breviceps* that might be indicative of a cryptic species (Smith et al. 2005). A common finding in molecular population studies has been catchment-specific mtDNA haplotypes with little evidence of dispersal among adjacent coastal catchments (Waters et al. 2001). Historical hydrographic patterns have been a key driver in determining the genetic structure of freshwater fish populations with examples of river capture (Waters et al. 2001; Waters et al. 2006). A main north-south discontinuity was found in the Canterbury galaxiid *G. vulgaris* and in the dwarf galaxiid *G. divergens* in the northern South Island, with "Canterbury" and "Marlborough" lineages, separated by the Kaikoura ranges (Waters & Wallis 2000; Burridge et al. 2006). The upland bully *Go. breviceps* for the most part shows catchment-specific haplotypes (Smith et al. 2005; Burridge et al. 2006), but shared haplotypes among two neighbouring catchments in the northern South Island (Burridge et al. 2006), and among two neighbouring catchments in the lower North Island (Smith et al. 2005).

The dwarf or dune lakes inanga *G. gracilis* have been considered lake-locked populations of *G. maculatus*, with separate conservation units in each lake (Ling et al. 2001), and are recognised as in serious decline (Anon. 2004b). Significant genetic differentiation was found among lake-locked populations of koaro *G. brevipinnis* (King et al. 2003). In the threatened mudfish *Neochanna diversus*, three population groupings have been identified among

North Island wetland populations in northern and southern Northland and in Waikato (Ling et al. 2001). In the nationally endangered Canterbury (South Island) mudfish *N. burrowsius*, a study of the mtDNA control region found low diversity, but significant genetic subdivision among northern and southern populations in eastern Canterbury, with most wild populations representing distinct management units (Davey et al. 2003).

Genetic diversity in New Zealand freshwater invertebrates

Catchment specific haplotypes were found in freshwater crayfish, koura, *Paranephrops zealandicus* in the South Island and *P. planifrons* in the North Island and northern South Island (Apte et al. 2007), and specifically for *P. planifrons* among neighbouring catchments in the central west North Island (Smith & Smith 2009, this issue). An unexpected finding was three lineages of koura with a cryptic west coast South Island group in addition to *P. planifrons* and *P. zealandicus* (Apte et al. 2007). High sequence divergences among samples of the amphipod *Paracalliope fluviatilis* from the North and South Islands, and among eastern and western catchments in the North Island, suggested a complex consisting of at least four, and perhaps as many as six, geographically isolated and morphologically conservative cryptic species (Hogg et al. 2006).

In contrast, a molecular population study of the mussel *Echyridella menziesi* found weak isolation by distance with the most common mtDNA haplotype shared among southern catchments, and by inference the mussels are strong dispersers with gene-flow among catchments via fish hosts (Fenwick 2006). Shell morphology has shown significant differences among six lake populations in the central North Island (Roper & Hickey 1994), but morphological variation may represent phenotypic rather than genotypic variation.

Among the winged insects, some species appear to be strong dispersers. Three species of damselflies (Odonata: *Xanthocnemis*, *Austrolestes*, and *Ischnura*) in which the adults are relatively long-lived (and two are found on offshore islands) show low population differentiation leading to the conclusion that levels of gene flow within the North and South islands have been sufficient to maintain homogeneous population structures (Nolan et al. 2007). In contrast, the mayfly *Acanthophlebia cruentata* and the caddisfly *Orthopsyche fimbriata*, restricted to native forest streams in the North Island, exhibit genetically differentiated populations among catchments at the 70–100 km scale (Smith & Collier 2001; Smith et al. 2006a,b). A hierarchical analysis of *O. fimbriata* populations from 14 streams in eight neighbouring catchments in the central west North Island found high haplotype diversity with c. 56% of genetic diversity distributed among catchments (Smith & Smith 2009). Haplotypes were shared across catchments and only the most northern and southern catchments, separated by straight line distances <100 km, did not share haplotypes (Smith & Smith 2009). In the mayfly *Coloburiscus humeralis*, low divergence and weak differentiation found with allozyme markers led to the conclusion that there is wide dispersal (Hogg et al. 2002). However, low allozyme diversity might provide a weak test of population differentiation; low population differentiation found with allozyme markers in *A. cruentata* (Smith & Collier 2001) contrasts with high mtDNA haplotype diversity, with 58% of variation distributed among catchments and catchment-specific haplotypes at the 70–100 km scale (Smith et al. 2006b).

In the megalopteran *Archicauliodes diversus* genetic differentiation was found among Northland and central North Island populations, whereas fixed genetic differences at some allozyme loci among North and South Island populations may be indicative of cryptic species (Hogg et al. 2002).

Guidelines for genetic restoration

Guidelines for genetic restoration have been developed for plant populations (McKay et al. 2005; Falk et al. 2006) and for commercially important fish and shellfish (FAO 1981, 1993; Munro 1993; Benzie & Williams 1996; Gaffney 2006). Most guidelines are species- and/or site-specific and emphasise that genetics cannot be considered in isolation from ecology, but should be an integral component of the restoration process (Geist & Kuehn 2005a). Genetic principles will not apply equally to all species and all restoration sites, therefore specific projects will need to be developed for each New Zealand location (Richardson & Jowett 2005; Jowett et al. 2009; Leathwick et al. 2009). Many translocations have failed to establish sustainable populations (Sheller et al. 2006), and in one example, translocation of the Australian freshwater shrimp *Paratya australiensis* accidentally mixed two ESUs in different sub-catchments leading to the expiration of resident genotypes within seven generations (Hughes et al. 2003). Less than half of the early (pre 1987) translocation efforts with birds and mammals were successful (Wolf et al. 1996), whereas 50–70% of

translocations of the endangered gila topminnow, *Poeciliopsis occidentalis*, in the southwest United States failed within the first 5 years (Sheller et al. 2006). Key factors that led to successful (= persistent) translocations of *Po. occidentalis* included the season in which the fish were translocated, the habitat type of the translocation site, and the genetic origin of the source population, leading the authors to emphasise that life-history attributes need to be considered for each translocated species (Sheller et al. 2006).

Rare and threatened species are more likely to require hatchery supplementation rather than translocation because sampling wild populations may further stress their status and provide insufficient numbers to establish viable populations. For an introduction of 50 individuals and assuming an initial survival of 30–50%, owing to mortalities during the collection, transport and release stages, 100–170 (50/0.5, 50/0.3) individuals would need to be collected (Brown & Briggs 1991; Falk et al. 2006). Removing 100+ individuals even from non-threatened populations may lead to local depletion, inadvertently creating a restoration problem in the donor population. Estimates of fish densities in New Zealand rivers are mostly for diadromous species and are typically low, <1 individual m^{-2}, range 0.008–3.0 individuals m^{-2} (Jowett et al. 1999; Chadderton & Allibone 2000; Rowe et al. 2002; West et al. 2005); although inanga *G. maculatus* may form dense schools with 500–1000 individuals in single pools (Jowett et al. 1998). Densities of diadromous *Gobiomorphus* are typically <1 individuals m^{-2} (Jowett & Richardson 1996; Jowett et al. 1996), whereas koura *Paranephrops* are 1–4 individuals m^{-2} (Rabeni et al. 1997; Olsson et al. 2006). Using several source populations from neighbouring streams in the same catchment (20 individuals × 5–8 streams) may reduce local depletion while providing a representative sample of catchment genetic diversity without risking outbreeding depression. Given high initial mortalities, the translocations may need to be repeated over several years.

Eldon (1993) recommended translocation of juveniles as opposed to adults of the nationally endangered eastern South Island Canterbury mudfish *N. burrowsius* owing to ease of capture and handling. The key ecological criteria that contributed to the successful liberation of *N. burrowsius* into ponds and their short-term persistence over a few years have been identified (Eldon 1993), and the Waianiwaniwa River, on the Canterbury Plains, has been identified as the most important refuge free of larger predatory fish and reduced competition from other fish species

(Harding et al. 2007). DNA studies have identified significant genetic structure that should be considered in future restoration projects (Davey et al. 2003).

Ultimately, restoration success will be dependent upon the application of ecological and genetic principles and will be measured by the persistence of restored populations over timescales beyond the working life span of most scientists.

REFERENCES

Allendorf F, Luikart G 2006. Conservation and the genetics of populations. Malden, United States, Blackwell Publishing. 664 p.

Allibone RM, Crowl TA, Holmes JM, King TM, McDowall RM, Townsend CR, Wallis GP 1996. Isozyme analysis of *Galaxias* species (Teleostei: Galaxiidae) from the Taieri River, South Island, New Zealand: a species complex revealed. Biological Journal of the Linnean Society 57: 107–127.

Anonymous 2003. New Zealand mudfish (*Neochanna* spp.) recovery plan (Northland, black, brown, Canterbury and Chatham mudfish). Threatened species recovery plan 51. Department of Conservation, Wellington, New Zealand. 27 p.

Anonymous 2004a. Aquatic habitat guidelines: an integrated approach to marine, freshwater, and riparian habitat protection and restoration. http://wdfw.wa.gov/hab/ahg/shrg/index.htm [accessed 20 November 2007].

Anonymous 2004b. New Zealand non-migratory galaxiid fishes recovery plan. Threatened species recovery plan 53. Department of Conservation, Wellington, New Zealand. 45 p.

Apte S, Smith PJ, Wallis GP 2007. Mitochondrial phylogeography of New Zealand freshwater crayfishes, *Paranephrops* spp. Molecular Ecology 16: 1897–1908.

Araguas RM, Roldán MI, García-Marín JL, Pla C 2007. Management of gene diversity in the endemic killifish *Aphanius iberus*: revising Operational Conservation Units. Ecology of Freshwater Fish 16: 257–266.

Ayllon F, Martinez J, Garcia-Vazquez E 2006. Loss of regional population structure in Atlantic salmon, *Salmo salar* L., following stocking. ICES Journal of Marine Science 63: 1269–1273.

Bartley DM, Bagley M, Gall G, Bentley B 1992. Use of linkage disequilibrium data to estimate effective population size of hatchery and natural fish populations. Conservation Biology 6: 365–375.

Bell M 2001. Lateral plate evolution in the threespine stickleback: getting nowhere fast. Genetica 112: 445–461.

Belshaw R, Bensasson D 2006. The rise and falls of introns. Heredity 96: 208–213.

Bensch S, Akesson M 2005. Ten years of AFLP in ecology and evolution: why so few animals? Molecular Ecology 14: 2899–2914.

Benzie J, Williams S 1996. Limitations in the genetic variation of hatchery produced batches of the giant clam *Tridacna gigas*. Aquaculture 139: 225–241.

Bilton DF, Okamura B 2001. Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics 32: 159–181.

Binks R, Kennington W, Johnson M 2007. Rapid evolutionary responses in a translocated population of intertidal snail (*Bembicium vittatum*) utilise variation from different source populations. Conservation Genetics 8: 1421–1429.

Blakely T, Harding J, McIntosh A, Winterbourn M 2006. Barriers to the recovery of aquatic insect communities in urban streams. Freshwater Biology 51: 1634–1645.

Bohonak A 1999. Dispersal, gene flow and population structure. Quarterly Review of Biology 74: 21–45.

Bonnell ML, Selander RK 1974. Elephant seals: genetic variation and near extinction. Science 184: 908–909.

Brown A, Briggs J 1991. Sampling strategies for genetic variation in ex situ collections of endangered plant species. In: Falk DA, Holsinger KE ed. Genetics and conservation of rare plants. New York, Oxford University Press. Pp. 99–118.

Burridge CP, Craw D, Waters JM 2006. River capture, range expansion, and cladogenesis: the genetic signature of freshwater vicariance. Evolution 60: 1038–1045.

Chadderton WL, Allibone RM 2000. Habitat use and longitudinal distribution patterns of native fish from a near pristine Stewart Island, New Zealand, stream. New Zealand Journal of Marine and Freshwater Research 34: 487–499.

Clewell A, Aronson J 2007. Ecological restoration: principles, values, and structure of an emerging profession. Washington DC, Island Press. 197 p.

Cook B, Bunn S, Hughes J 2007. Molecular genetic and stable isotope signatures reveal complementary patterns of population connectivity in the regionally vulnerable southern pygmy perch (*Nannoperca australis*). Biological Conservation 138: 60–72.

Crandall K, Bininda-Emonds O, Mace G, Wayne R 2000. Considering evolutionary processes in conservation biology. Trends in Ecology and Evolution 15: 290–295.

Davey M, O'Brien L, Ling N, Gleeson D 2003. Population genetic structure of the Canterbury mudfish (*Neochanna burrowsius*): biogeography and conservation implications. New Zealand Journal of Marine and Freshwater Research 37: 13–21.

De Guia APO, Saitoh T 2007. The gap between the concept and definitions in the Evolutionarily Significant Unit: the need to integrate neutral genetic variation and adaptive variation. Ecological Research 22: 604–612.

Demand M, Bjorklund M 2007. Loss of genetic variability in reintroduced roach (*Rutilus rutilus*) populations. Journal of Fish Biology 70B: 255–261.

de Winton MD, Clayton JS, Champion PD 2000. Seedling emergence from seed banks of 15 New Zealand lakes with contrasing vegetation histories. Aquatic Botany 66: 181–194.

Dewoody JA, Avise JC 2000. Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. Journal of Fish Biology 56: 461–473.

Dionne M, Dodson JJ, Bernatchez L, Miller KM, Caron F 2007. Clinal variation in MHC diversity with temperature: evidence for the role of host-pathogen interaction on local adaptation in Atlantic salmon. Evolution 61: 2154–2164.

Dunn N, O'Brien L 2005. Captive management of mudfish *Neochanna* (Teleostei: Galaxiidae) spp. Department of Conservation, Wellington, New Zealand. Research and Development Series 205. 29 p.

Elderkin C, Christian A, Metcalfe-Smith J, Berg D 2008. Population genetics and phylogeography of freshwater mussels in North America, *Elliptio dilatata* and *Actinonaias ligamentina* (Bivlavia: Unionidae). Moelcular Ecology 17: 2149–2163.

Eldon G 1993. Guidelines towards a conservation strategy for the Canterbury mudfish (*Neochanna burrowsius*). New Zealand Freshwater Research Report 4. 19 p.

Endler J 1977. Geographic variation, speciation, and clines. Monographs in Population Biology 10. 246 p.

Endler J 1986. Natural selection in the wild. Princeton, New Jersey, Princeton University Press. 354 p.

Falk D, Richards C, Montalvo A, Knapp E 2006. Population and ecological genetics in restoration ecology. In: Falk DA, Palmer MA, Zedler JB ed. Foundations for Restoration Ecology. Pp. 14–41.

FAO 1981. Conservation of the genetic resources of fish: problems and recommendations. Food and Agriculture Organization Fisheries Technical Paper 217. 43 p.

FAO 1993. Report of the expert consultation on utilization and conservation of aquatic genetic resources. Food and Agriculture Organization Fisheries Report 491. 59 p.

Ford M 2002. Applications of selective neutrality tests to molecular ecology. Molecular Ecology 11: 1245–1262.

Fenwick M 2006. The molecular phylogenetics of the New Zealand freshwater mussels. Unpublished MSc thesis, Victoria University of Wellington, New Zealand. 113 p.

Finn DS, Adler PH 2006. Population genetic structure of a rare high-elevation black fly, *Metacnephia coloradensis*, occupying Colorado lake outlet streams. Freshwater Biology 51: 2240–2251.

Frankham R 1995a. Effective population size/adult population size ratios in wildlife. Genetical Research 66: 95–107.

Frankham R 1995b. Inbreeding and extinction: a threshold effect. Conservation Biology 9: 792-799.

Frankham R, Ballou J, Briscoe D 2004. A primer of conservation genetics. Cambridge, United Kingdom, Cambridge University Press. 234 p.

Franklin I 1980. Evolutionary change in small populations. In: Soule M, Wilcox B ed. Conservation Biology. Pp. 135–150.

Fraser D, Bernatchez L 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Molecular Ecology 10: 2741–2752.

Gaffney PM 2006. The role of genetics in shellfish restoration. Aquatic Living Resources 19: 277–282.

Geist J, Kuehn R 2005. Genetic diversity and differentiation of central European freshwater pearl mussel (*Margaritifera margaritifera* L.) populations: implications for conservation and management. Molecular Ecology 14: 425–439.

Gleeson D, Howitt R, Ling N 1999. Genetic variation, population structure and cryptic species within the black mudfish *Neochanna diversus* an endemic galaxiid from New Zealand. Molecular Ecology 8: 47–57.

Gyllenstein U 1985. The genetic structure of fish: differences in the intraspecific distribution of biochemical genetic variation between marine, anadromous, and freshwater species. Journal of Fish Biology 26: 691–699.

Hansen MM, Jensen LF, Bekkevold D, Mensberg K-LD, Skaala O, Jensen LF 2007. Gene flow, effective population size and selection at major histocompatibility complex genes: brown trout in the Hardanger Fjord, Norway. Molecular Ecology 16: 1413–1425.

Harding J, Norton D, McIntosh A 2007. Persistence of a significant population of rare Canterbury mudfish (*Neochanna burrowsius*) in a hydrologically isolated catchment. New Zealand Journal of Marine and Freshwater Research 41: 309–316.

Hedrick PW 1999. Perspective: highly variable loci and their interpretation in evolution and conservation. Evolution 53: 311–318.

Hedrick P 2005. 'Genetic restoration:' a more comprehensive perspective than 'genetic rescue'. Trends in Ecology and Evolution 20: 109.

Hedrick PW, Hedgecock D, Hamelburg S 1995. Effective population size in winter run Chinook salmon. Conservation Biology 9: 615–624.

Hedrick PW, Rashbrook VK, Hedgecock D 2000. Effective population size of winter-run chinook salmon based on microsatellite analysis of returning spawners. Canadian Journal of Fisheries and Aquatic Sciences 57: 2368–2373.

Hindar K, Ryman N, Utter F 1991. Genetic effects of cultured fish on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48: 945–957.

Hogg I, Stevens M, Schnabel K, Chapman M 2006. Deeply divergent lineages of the widespread New Zealand amphipod *Paracalliope fluviatilis* revealed using allozyme and mitochondrial DNA analyses. Freshwater Biology 51: 236–248.

Hogg I, Willmann-Huerner P, Stevens M 2002. Population genetic structures of two New Zealand stream insects: *Achichauliodes diversus* (Megaloptera) and *Coloburiscus humeralis* (Ephemeroptera). New Zealand Journal of Marine and Freshwater Research 36: 491–501.

Hughes JM 2007. Constraints on recovery: using molecular methods to study connectivity of aquatic biota in rivers and streams. Freshwater Biology 52: 616–631.

Hughes J, Goudkamp K, Hurwood D, Hancock M, Bunn S 2003. Translocation causes extinction of a local population of the freshwater shrimp *Paratya australiensis*. Conservation Biology 17: 1007–1012.

Hurwood D, Hughes J, Bunn S, Cleary C 2003. Population structure in the freshwater shrimp (*Paratya australiensis*) inferred from allozymes and mitochondrial DNA. Heredity 90: 64–70.

ICES 1996. Report of the working group on introductions and transfers of marine organisms. International Council for the Exploration of the Sea, Denmark. ICES CM 1996/ENV:8. 89 p.

Johnson J, Belk M 2007. What the status of Utah chub tells us about conserving common, widespread species. American Fisheries Society Symposium 53. Pp. 165–173.

Jowett I, Richardson J 1996. Distribution and abundance of freshwater fish in New Zealand rivers. New Zealand Journal of Marine and Freshwater Research 30: 239–255.

Jowett I, Richardson J, McDowall R 1996. Relative effects of in-stream habitat and land use on fish distribution and abundance in tributaries of the Grey River, New Zealand. New Zealand Journal of Marine and Freshwater Research 30: 463–475.

Jowett I, Hayes J, Deans N, Eldon G 1998. Comparison of fish communities and abundance in unmodified streams of Kahurangi National Park with other areas of New Zealand. New Zealand Journal of Marine and Freshwater Research 32: 307–322.

Jowett I, Richardson J, McDowall R 1999. Relative effects of in-stream habitat and land use on fish distribution and abundance in tributaries of the Grey River, New Zealand. New Zealand Journal of Marine and Freshwater Research 30: 463–475.

Jowett IG, Richardson J, Boubée JAT 2009. Effects of riparian manipulation on stream communities in small streams: two case studies. New Zealand Journal of Marine and Freshwater Research 43: 763–774 (this issue).

Katz L, Barnas K, Hicks R, Cowen J, Jenkinson R 2007. Freshwater habitat restoration actions in the Pacific northwest: a decade's investment in habitat improvement. Restoration Ecology 15: 494–505.

King K, Young K, Waters J, Wallis G 2003. Preliminary genetic analysis of koaro (*Galaxias brevipinnis*) in New Zealand lakes: evidence for allopatric differentiation among lakes but little population subdivision within lakes. Journal of the Royal Society of New Zealand 33: 591–600.

Kliber A, Eckert C 2005. Interaction between founder effect and selection during biological invasion in an aquatic plant. Evolution 59: 1900–1913.

Lacy R 1997. Importance of genetic variation to the viability of mammalian populations. Journal of Mammalogy 78: 320–325.

Lande R 1995. Risk of population extinction from fixation of new deleterious mutations. Evolution 48: 1460–1469.

Langefores A, von Schantz T, Widegren B 1998. Allelic variation of Mhc class 11 in Atlantic salmon: a population genetic analysis. Heredity 80: 568–575.

Larsen PN, Nielsen EE, Williams TD, Hemmer-Hansen J, Chipman JK, Kruhoffer M, Gronkjaer P, George SG, Dyrskjot L, Loeschcke V 2007. Adaptive differences in gene expression in European flounder (*Platichthys flesus*). Molecular Ecology 16: 4674–4683.

Leathwick JR, Elith J, Rowe D, Julian K 2009. Robust planning for restoring diadromous fish species in New Zealand's lowland rivers and streams. New Zealand Journal of Marine and Freshwater Research 43: 659–671 (this issue).

Ling N, Gleeson DM, Wilson KJ, Binzegger SU 2001. Creating and destroying species: the "new" biodiversity and evolutionary significant units among New Zealand's galaxiid fishes. Journal of Fish Biology 59 (Suppl. A): 209–222.

Lynch M 1996. A quantitative genetic perspective on conservation issues. In: Avise JC, Hamrick J ed. Conservation genetics: case histories from nature. New York, Chapman and Hall. Pp. 471–501.

Lynch M 2005. Inbreeding depression and outbreeding depression. In: Grant WS ed. Genetic effects of straying of non-native hatchery fish into natural populations. US Department of Commerce, NOAA Technical Memorandum. NMFS-NWFSC-30. 130 p.

Lynch M, Conery J, Buerger R 1995. Mutation accumulation and the extinction of small populations. American Naturalist 146: 489–518.

Lynch MP, Pfreinder M, Spitze K, Lehman N, Hicks J, Allen D, Latta L, Ottene M, Bogue F, Colbourne J 1999. The quantitative and molecular genetic architecture of a subdivided species. Evolution 53: 100–110.

Malmqvist B 2002. Aquatic invertebrates in riverine landscapes. Freshwater Biology 47: 679–694.

Manel S, Schwartz M, Luikart P, Taberlet P 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology and Evolution 18: 189–197:

McDowall R, Waters J 2002. A new longjaw *galaxias* species (Teleostei: Galaxiidae) from the Kauru River, North Otago, New Zealand. New Zealand Journal of Zoology 29: 41–52.

McDowall R, Waters J 2003. A new species of *Galaxias* (Teleostei: Galaxiidae) from the Mackenzie Basin, New Zealand. Journal of the Royal Society of New Zealand 33: 675–691.

McKay JK, Christian CE, Harrison S, Rice KJ 2005. 'How local is local?'—a review of practical and conceptual issues in the genetics of restoration. Restoration Ecology 13: 432–440.

Miller LM, Kapuscinski AR 1997. Historical analysis of genetic variation reveals low effective population size in northern pike (*Esox lucius*) population. Genetics 147: 1249–1258.

Mitton J 1997. Selection in natural populations. Oxford, Oxford University Press. 272 p.

Monaghan T, Spaak P, Robinson C, Ward J 2001. Genetic differentiation of *Baetis alpinus* Pichet (Ephemeroptera: Baetidae) in fragmented alpine streams. Heredity 86: 395–403.

Moritz C 1994. Defining "evolutionary significant units" for conservation. Trends in Ecology and Evolution 9: 373–375.

Munro P ed. 1993. Genetic aspects of conservation and cultivation of giant clams. International Center for Living Aquatic Resources Management Conference Proceedings 39. 47 p.

Nei M 1973. Analysis of gene diversity in subdivided populations. Proceedings of the National Academy of Sciences 70: 3321–3323.

Nei M 1987. Molecular evolutionary genetics. New York, Columbia University Press. 512 p.

Nolan L, Hogg I, Sutherland D, Stevens M, Schnabel K 2007. Allozyme and mitochondrial DNA variability within the New Zealand damselfly genera *Xanthocnemis*, *Austrolestes*, and *Ischnura* (Odonata). New Zealand Journal of Zoology 34: 371–380.

Nunney L, Campell A 1993. Assessing minimum viable population size: demography meets population genetics. Trends in Ecology and Evolution 8: 234–239.

Olsson K, Stenroth P, Nyström P, Holmqvist N, McIntosh A, Winterbourn M 2006. Does natural acidity mediate interactions between introduced brown trout, native fish, crayfish and other invertebrates in West Coast New Zealand streams? Biological Conservation 130: 255–267.

Page KS, Scribner KT, Bast D, Holey ME, Burnham-Curtis MK 2005. Genetic evaluation of a Great Lakes lake trout hatchery program. Transactions of the American Fisheries Society 134: 872–891.

Pogson G, Mesa K 2004. Positive Darwinian selection at the pantophysin (Pan I) locus in marine gadid fishes. Molecular Biology and Evolution 21: 65–75.

Rabeni C, Collier K, Parkyn S, Hicks B 1997. Evaluating techniques for sampling stream crayfish (*Paranephrops planifrons*). New Zealand Journal of Marine and Freshwater Research 31: 693–700.

Ramp JM, Collinge SK, Ranker TA 2006. Restoration genetics of the vernal pool endemic *Lasthenia conjugens* (Asteraceae). Conservation Genetics 7: 631–649.

Reed D, Bryant E 2000. Experimental tests of minimum viable population size. Animal Conservation 3: 7–14.

Reed D, O'Grady J, Brook B, Ballou J, Frankham R 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. Biological Conservation 113: 23–42.

Reznick DA, Shaw F, Rodd FH, Shaw RG 1997. Evaluation of the rate of evolution in natural population of guppies (*Poecilia reticulata*). Science 275: 1934–1937.

Richardson J, Jowett I 2005. Restoring streams for freshwater fish. National Institute of Water and Atmospheric Research Ltd, Hamilton, New Zealand. NIWA Science and Technology Series 53. 55 p.

Rogers S, Isabel N, Bernatchez L 2007. Linkage maps of the dwarf and normal lake whitefish (*Coregonus clupeaformis*) species complex and their hybrids reveal the genetic architecture of population divergence. Genetics 175: 375–398.

Roper D, Hickey C 1994. Population structure, shell morphology, age and condition of the freshwater mussel *Hyridella menziesi* (Unionacea: Hyriidae) from seven lake and river sites in the Waikato River system. Hydrobiologia 284: 205–217.

Rowe D, Smith J, Quinn J, Boothroyd I 2002. Effects of logging with and without riparian strips on fish species abundance, mean size, and the structure of native fish assemblages in Coromandel, New Zealand, streams. New Zealand Journal of Marine and Freshwater Research 36: 67–79.

Ryder OA 1986. Species conservation and systematics: the dilemma of subspecies. Trends in Ecology and Evolution 1: 9–10.

Ryman N 1991. Conservation genetics considerations in fishery management. Journal of Fish Biology 39: 211–224.

Schöffmann J, Sušnik S, Snoj A 2007. Phylogenetic origin of *Salmo trutta* L. 1758 from Sicily, based on mitochondrial and nuclear DNA analyses. Hydrobiologia 575: 51–55.

Sheller FJ, Fagan WF, Unmack PJ 2006. Using survival analysis to study translocation success in the Gila topminnow (*Poeciliopsis occidentalis*). Ecological Applications 16: 1771–1784.

Slatkin M 1987. Gene flow and the geographic structure of natural populations. Science 236: 787–792.

Smith PJ, Collier KJ 2001. Allozyme diversity and population structure of the caddisfly *Orthopsyche fimbriata* and the mayfly *Acanthophlebia cruenta* in New Zealand streams. Freshwater Biology 46: 795–805.

Smith PJ, Smith BJ 2009. Small-scale population-genetic differentiation in the New Zealand caddisfly *Orthopsyche fimbriata* and the crayfish *Paranephrops planifrons*. New Zealand Journal of Marine and Freshwater Research 43: 723–734 (this issue).

Smith MH, Smith MW, Scott SL, Liu EH, Jones JC 1983. Rapid evolution in a post-thermal environment. Copeia 1983: 193–197.

Smith PJ, McVeagh M, Allibone R 2005. Extensive genetic differentiation in *Gobiomorphus breviceps* Pisces: Gobiidae) from New Zealand. Journal of Fish Biology 67: 627–639.

Smith PJ, McVeagh SM, Collier KJ 2006a. Population-genetic structure in the New Zealand caddisfly *Orthopsyche fimbriata* revealed with mitochondrial DNA. New Zealand Journal of Marine and Freshwater Research 40: 141–148.

Smith P, McVeagh S, Collier K 2006b. Genetic diversity and historical population structure in the New Zealand mayfly *Acanthophlebia cruentata*. Freshwater Biology 51: 12–24.

Soule M 1988. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, United States. 584 p.

Stockwell C, Weeks S 1999. Translocations and rapid evolutionary repsonses in recently established populations of western mosquitofish (*Gambusia affinis*). Animal Conservation 2: 103–110.

Takagawa S, Washitani I, Uesugi R, Tsumura Y 2006. Influence of inbreeding depression on a lake population of *Nymphoides peltata* after restoration from the soil seed bank. Conservation Genetics 7: 705–716.

Tallmon DA, Luikart G, Waples RS 2004. The alluring simplicity and complex reality of genetic rescue. Trends in Ecology and Evolution 19: 489–496.

Utter FM 2004. Population genetics, conservation and evolution in salmonids and other widely cultured fishes: some perspectives over six decades. Reviews in Fish Biology and Fisheries 14: 125–144.

Vasemagi A, Gross R, Paaver T, Koljonen ML, Saisa M, Nilsson J 2005. Analysis of gene associated tandem repeat markers in Atlantic salmon (*Salmo salar* L.) populations: implications for restoration and conservation in the Baltic Sea. Conservation Genetics 6: 385–397.

Verspoor E, de Leaniz C, McGinnity P 2007. Genetics and habitat management. In: Verspoor E, Stradmeyer L, Nielsen JL ed. The Atlantic salmon: genetics, conservation and management. Pp. 399–424.

Visscher PM, Smith D, Hall SJG, Williams JA 2001. A viable herd of genetically uniform cattle. Nature 409: 303.

Vrijenhoek RC 1998. Conservation genetics of freshwater fish. Journal of Fish Biology 53(Suppl. A): 394–412.

Waples RS 1995. Evolutionary significant units and the conservation of biological diversity under the Enangered Species Act. American Fisheries Society Symposium 17: 8–27.

Waples RS, Gaggiotti O 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Molecular Ecology 15: 1419–1439.

Ward RD, Woodwark M, Skibinski DOF 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. Journal of Fish Biology 44: 213–232.

Waters J, Wallis G 2000. Across the Southern Alps by river capture? Freshwater fish phylogeography in South Island, New Zealand. Molecular Ecology 9: 1577–1582.

Waters J, Wallis G 2001. Mitochondrial DNA phylogenetics of the *Galaxiias vulgaris* complex from South Island, New Zealand: rapid radiation of a species flock. Journal of Fish Biology 58: 1166–1180.

Waters JM, Allibone RM, Wallis GP 2006. Geological subsidence, river capture, and cladogenesis of galaxiid fish lineages in central New Zealand. Biological Journal of the Linnean Society 88: 367–376.

Waters JM, Craw D, Youngson JH, Wallis GP 2001. Genes meet geology: fish phylogeographic pattern reflects ancient, rather than modern, drainage conenctions. Evolution 55: 1844–1851.

West D, Jowett I, Richardson J 2005. Growth, diet, movement, and abundance of adult banded kokopu (*Galaxias fasciatus*) in five Coromandel, New Zealand streams. New Zealand Journal of Marine and Freshwater Research 39: 915–929.

Wilson CC, Lavender M, Black J 2007. Genetic assessment of walleye (*Sander vitreus*) restoration efforts and options in Nipigon Bay and Black Bay, Lake Superior. Journal of Great Lakes Research 33: 133–144.

Winterbourn M, Harding J, McIntosh A 2007. Response of the benthic fauna of an urban stream during six years of restoration. New Zealand Natural Sciences 32: 1–12.

Wolf C, Griffith B, Reed C, Temple S 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10: 1142–1154.

Wright S 1940. Breeding structure of populations in relation to speciation. American Naturalist 74: 232–248.

Wright S 1951. The genetical structure of populations. Annals of Eugenics 15: 323–354.