

Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts

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Abstract

By providing new approaches to the investigation of demographic and evolutionary dynamics of wild populations, molecular genetics has led to fundamental changes in our understanding of marine ecology. In particular, genetic approaches have revolutionized our understanding in three areas: (i) most importantly, they have contributed to the discovery of extensive genetic population structure in many marine species, overturning the notion of large, essentially homogenous marine populations limiting local adaptation and speciation. (ii) Concomitant differences in ecologically important traits now indicate extensive adaptive differentiation and biocomplexity, potentially increasing the resilience to exploitation and disturbance. Evidence for rapid adaptive change in many populations underlies recent concerns about fisheries-induced evolution affecting life-history traits. (iii) A compilation of recent published research shows estimated effective population sizes that are 2–6 orders of magnitude smaller than census sizes, suggesting more complex recruitment dynamics in marine species than previously assumed. Studies on Atlantic cod are used to illustrate these paradigm shifts. In our synthesis, we emphasize the implications of these discoveries for marine ecology and evolution as well as the management and conservation of exploited marine fish populations. An important implication of genetic structuring and the potential for adaptive divergence is that locally adapted populations are unlikely to be replaced through immigration, with potentially detrimental consequences for the resilience to environmental change – a key consideration for sustainable fisheries management.

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Introduction	334
Population structure in marine fishes	335
Paradigm shift	335
Genetic differentiation in space and time	336
Population connectivity in marine fishes on a fine scale	338
Spatial and temporal scale of adaptation	339
Paradigm shifts	339
Spatial scale of adaptive differentiation	340
Temporal scale of adaptive differentiation	342

Population size in marine fishes	343
Paradigm shift	343
Biological mechanisms leading to low N_e/N ratios	343
Implications and significance of small effective population sizes	347
Atlantic cod as a case study for the paradigm shifts	349
Concluding remarks	351
Acknowledgements	351
References	352

Introduction

Fisheries genetics – the application of genetic principles and methods to fisheries biology and management – has stimulated a resurgence of interest in the factors underpinning the dynamics and resilience of exploited species. Topics such as connectivity among marine populations (Cowen *et al.* 2006; Trembl *et al.* 2008), the spatial and temporal scale of population differentiation (Jørgensen *et al.* 2005; Ruzzante *et al.* 2006), effective population size (Hauser *et al.* 2002; Waples and Yokota 2007), fisheries-induced evolution (Marshall and Browman 2007) and the analysis of adaptive variation in the wild (Conover *et al.* 2006) not only enhance our understanding of the mechanisms shaping fish abundance and distribution, but also contribute conceptually to ecological and evolutionary theory. Whereas classical fisheries approaches typically focused on factors driving short-term demographic changes in populations ('quantitative' change), genetic approaches examine the extent to which changes in the composition of populations ('qualitative' change) influence both short-term alterations in phenotypic traits and longer-term response to natural and anthropogenic perturbations (Frankham 2005). Although the notion that population dynamics and genetic structure are inextricably linked was emphasized long ago (Elton 1924), traditional fisheries biology makes scant reference to genetic factors in fish population ecology, as evidenced by recent texts in the area (Jennings *et al.* 2001; but see Hallerman 2003). Yet, as is clear from the recent boom in publications in the field (Kochzius *in press*), the incorporation of such 'qualitative' thinking into fish and fisheries biology has generated new insights into the temporal and spatial scale of change in fish populations and communities (Conover *et al.* 2006; Larsen *et al.* 2007), culminating in a considerable shift in how

we view both the marine environment and some of its key inhabitants.

The classical notion that marine environments tend to be demographically 'open,' and that many species have either high mobility or potential for dispersal during the egg and larval stages, coincided with many early genetic studies that typically indicated a lack of genetic differentiation across often even wide geographic scales (Ward *et al.* 1994). Associated with such general patterns was the expectation, as famously pronounced by Thomas Huxley in 1883, that 'a number of the most important sea fisheries, such as the cod fishery, the herring fishery, and the mackerel fishery, are inexhaustible' (Jennings *et al.* 2001). The implication was that most marine fish populations have vast population sizes that would not be subjected to either rapid or stochastic genetic change. The predominant evolutionary forces affecting marine fish genetic structure were considered to be selection and gene flow, resulting in expectations of populations exhibiting modest rates of evolutionary change. With wide distribution, extensive larval and adult dispersal and large population size, opportunities for local adaptation would be constrained by high migration and exposure to a breadth of environments.

Recently, however, genetic studies have challenged such traditional views by demonstrating population subdivision in marine fishes on a limited geographical scale ranging from tens to a few hundred kilometres (Ruzzante 1998; Knutsen *et al.* 2003; Nielsen *et al.* 2004; Olsen *et al.* 2008). Although such genetic differentiation tends to be much smaller in marine than in freshwater and terrestrial species (Waples 1998), and is often barely statistically significant, its biological relevance can be (and has been) demonstrated by correlation with environmental factors (Bekkevold *et al.* 2005), and by temporal and spatial replication (Cimmaruta

et al. 2008). The adaptive significance of population structure in marine fishes is increasingly becoming evident by reports of divergence at phenotypic traits, often even despite the lack of neutral genetic differentiation (Hutchings *et al.* 2007). Additionally, recent data now indicate that genetically effective population sizes (N_e) in marine fishes, especially those characterized by high fecundity and high larval mortality, are typically 2–6 orders of magnitude smaller than census population sizes. Such insights from genetic data have profound implications for both our understanding of the demography of marine species and the management and conservation of exploited living resources. It thus appears timely to examine the impact of findings from molecular genetics on marine fish and fisheries biology.

Here, we address three primary questions:

1. *Which fundamental paradigms in fisheries biology have been overthrown by genetic data over the past decades?* Although genetic research had an impact on a variety of topics, including the resolution of taxonomic uncertainties, description of long-term demographic dynamics and the development of the theory of evolutionary change, we will concentrate on three major issues: identification of population structure, assessment of spatial and temporal scales of adaptation and estimation of population sizes.
2. *What is our current view of underlying mechanisms that drive the observed patterns of population diversity and abundance based on genetic data?* Much past effort has been expended on descriptive analysis of populations, yielding data on patterns of stock distribution and abundance, with relatively little opportunity for exploration of underlying mechanisms. Through a combination of new molecular tools and analytical approaches, it is now possible to explore more rigorously the role of physical and biological factors affecting dynamics and distribution.
3. *To what extent are such insights relevant to the management and conservation of marine fish and fisheries?* While such paradigm shifts are interesting scientifically and can provide a better understanding of species biology, they also have important consequences for fisheries management.

Our aim is not to provide an exhaustive review of recent studies in the field, which is provided elsewhere (e.g. Hallerman 2003; Hedgecock *et al.*

2008; Kochzius *in press*), but rather to consider critically the impact of recent genetic applications on concepts that have dominated much of our thinking in marine fisheries ecology. Although major challenges remain to our understanding of the primary forces shaping patterns of genetic variability in marine fishes, resulting in controversies of their implications for management and conservation, we highlight instances where clarity and detail have been enhanced, rather than claiming that findings are necessarily typical. Because of the nature of molecular genetic markers, negative results (lack of population differentiation, infinite estimates of population size) are usually inconclusive in ecological terms – where patterns are found, however, they can be particularly relevant for fisheries ecology and management (Bentzen 1998).

Population structure in marine fishes

Paradigm shift

Fisheries genetics has been dominated by the quest to delimit the boundaries of putative fishery stocks – key units in the management of sustainable fisheries. The idea that marine fish species should be managed at some subspecific level can be traced to the early 20th century when two pioneering fishery biologists, Heincke (1889) and Hjort (1914), established the local self-sustaining population as opposed to typological species as the preferred unit of study for fisheries management. The classical notion of marine fishes occupying ‘open’ environments, with extensive gene flow and infinite population size, has shifted. Although such cases of wide-scale genetic homogeneity appear to exist (Mariani *et al.* 2005; Cassista and Hart 2007), there has been an escalation of instances where genetic structuring is evident, even across small spatial scales (Ruzzante *et al.* 2000b; Jørgensen *et al.* 2005; Knutsen *et al.* 2007). Although there is almost certainly a publication bias for studies detecting such differentiation, these examples show that extensive population structure in apparently homogenous species does indeed exist.

Three primary drivers demand information at such scales. First, it is generally recognized that populations are the natural unit of evolutionary change, and as such provide the genetic resources required for adaptive response to natural and man-made changes in the environment (Bonin

et al. 2007). It is therefore at the level of populations that genetic and ecological diversity should be described for conservation measures, which necessitates discrimination between populations in relation to their distribution and abundance across regional waters. To preserve the evolutionary legacy and future evolutionary potential of a given marine fish species, it is important to secure viable populations covering the full geographical and environmental range (Nelson and Soulé 1987). The existence of biologically differentiated populations, so-called 'biocomplexity' (Michener *et al.* 2001), even in marine pelagic fishes (Mitchell 2006; Ruzzante *et al.* 2006), has been credited with a major role in conferring resilience and in buffering overall productivity of fish population complexes (Hilborn *et al.* 2003). Thus, a key aim of sustainable fisheries management is to identify the spatial and temporal scale of population structuring, and to devise tools to monitor its dynamics and contribution to overall fisheries production. Even apparently small genetic differences among populations of marine fishes at presumably neutral genetic markers could translate into important adaptive variation distributed among populations (Conover *et al.* 2006).

Second, it is at the population level that policy legislation and associated enforcement ideally should take place, although, in reality, logistic constraints often necessitate the application of management measures to multiple stocks (Waples *et al.* 2008). There is an increasing requirement for traceability of fish and fish products, both for consumer protection (Logan *et al.* 2008) and for regulatory enforcement (Primmer *et al.* 2000), in particular with respect to illegal, unreported and unregulated fishing (McCluskey and Lewison 2008). Ideally, fish products are not only identified to species, but also traced back to the population of origin (Ogden 2008). For example, in the UK, the Marine Stewardship Council encourages consumers to eat particular landings of cod that are taken from 'stocks maintained within safe limits.' Although the identification of the population of origin is limited by low genetic differentiation in marine fishes (Manel *et al.* 2002, 2005; Hauser *et al.* 2006), such approaches have already been used to estimate population contributions to mixed-stock feeding assemblages of Atlantic cod (*Gadus morhua*, Gadidae; Ruzzante *et al.* 2000a) and herring (*Clupea harengus*, Clupeidae; Ruzzante *et al.*

2006). Selected markers showing typically higher levels of differentiation (Pogson and Fevolden 2003; Moen *et al.* 2008) will further improve the power and applicability of such tests in marine species.

Third, overfishing, eutrophication and habitat disturbance have made it increasingly important to know which populations act as sources and sinks, and how they might be connected by larval and adult exchange. There is increasing awareness that spatially defined management in the form of marine protected areas (MPAs) is a key addition to the arsenal of methods to promote sustainability and for biodiversity conservation (Polunin 2002; Jones *et al.* 2008). Decisions governing the choice of reserve size, number, spacing and location depend heavily on species-specific patterns of connectivity, dispersal and biologically significant population structuring. Thus, taking into account the pivotal role of population structuring in management, conservation and enforcement, it is no surprise that there continues to be considerable investment in genetic studies targeted at stock discrimination (Kochzius *in press*).

Genetic differentiation in space and time

Despite the significance of the stock concept for fisheries management, there are few quantitative criteria for the definition of populations. Population structure ranges not only across a spatial continuum from complete isolation to complete panmixia (random mating) (Waples 1998; Waples and Gaggiotti 2006), but also a temporal continuum of recent evolutionary history from secondary contact between isolated populations to the recent separation of a single population into different subpopulations (Fig. 1). It is thus not surprising that stocks as units of fishery management, even if defined as biological entities (Carvalho and Hauser 1994), might differ considerably from populations identified by molecular markers (Waples *et al.* 2008).

Most importantly, genetic populations are defined by the number of migrants ($N_e m$, effective population size $N_e \times$ migration rate m), not by their migration rate (m) as for fishery stocks or ecological populations (Waples and Gaggiotti 2006; Waples *et al.* 2008). For example, consider a molecular approach that has the power to detect significant genetic differentiation (F_{ST} ; defined as the fraction of total genetic variation attributable to differences among populations) as low as $F_{ST} = 0.002$.

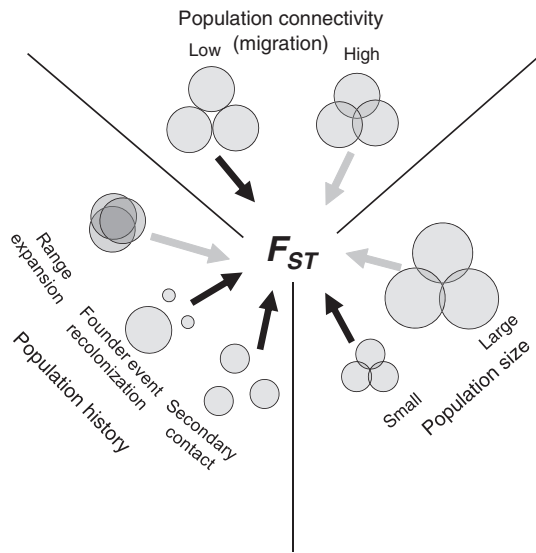


Figure 1 Conceptual diagram showing the influence of various factors (connectivity, history and size) on levels of genetic differentiation (measured by F_{ST}) in non-equilibrium populations. Grey arrows show a negative relationship, i.e. the respective factor reduces extant differentiation, while black arrows designate relationships likely to promote differentiation. Note that each of the various parameters represents a continuum – only the extremes are shown. Fisheries management is primarily interested in population connectivity, or the independence of stocks, while F_{ST} depends on other factors too. Selective effects are not considered here.

Although considerable caution should be used when estimating contemporary migration from genetic differentiation because of very restrictive assumptions of the underlying model (Whitlock and McCauley 1999), theoretically such an F_{ST} corresponds roughly to a gene flow of just over 120 individuals per generation (Wright 1931). In large populations ($N_e = 10^5$), 120 migrants would constitute a migration rate of only 0.12%. Migration rates between 0.2% and 10% would thus be sufficiently low to cause independent reaction of populations to demographic perturbation (Hastings 1993), but would be too high to allow the identification of such populations by molecular markers. Only if population sizes are as small as 1000 individuals ($N_e = 10^3$) would all ecologically relevant populations ($m < 10\%$) be identifiable with genetic methods ($N_e m < 100$, Fig. 2). It follows that in marine species with presumably large population sizes, most ecologically relevant population structure remains undetectable by

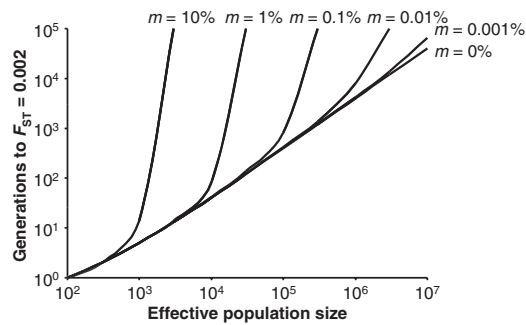


Figure 2 Time required for F_{ST} (measure of population differentiation) to reach 0.002, a level that is statistically significant from zero with commonly used approaches, under different migration rate (m , fraction of individuals exchanged each generation) scenarios. In large populations, several thousand generations are required to achieve that level of F_{ST} , even under complete isolation ($m = 0$). Calculated using Equation 7.11a in Hedrick (2000).

genetic markers (Bentzen 1998). It is also evident that, given similar migration rates (m), smaller populations are easier to identify by genetic means than larger ones – this theoretical prediction may explain reports of small outlier populations in otherwise relatively homogenous species (Beacham *et al.* 2002a; Buonaccorsi *et al.* 2002, 2005; Mitchell 2006; Cunningham *et al.* in press; Lin *et al.* 2008).

Another important consideration is the time scale of different population concepts and the methods of identifying them. Units of fisheries management are based on short-term reactions to exploitation, determined by year-to-year recruitment and short-term migration of large sectors of the populations. Genetic population differentiation, on the other hand, is related to migration integrated over extensive time periods, and can thus be affected by past, as well as contemporary, patterns of dispersal (Benzie 1999, 2000). In most temperate marine species, which might not have had sufficient time since the end of the last ice age to reach migration – drift equilibrium (balance of genetic differentiation between genetic drift and migration), contemporary genetic patterns may reflect not only extant forces, but also the number and size of glacial refugia (Hickerson and Ross 2001) and the patterns of recolonization to current distributions (Hewitt 2004). For example, if colonization occurs in the form of small founder events, significant, although possibly ephemeral, genetic differentiation can emerge (Dupont *et al.* 2003;

Herborg *et al.* 2007). If colonization happens simply by range expansion, genetic differentiation may occur because mutations arising at the edge of the expansion wave attain much higher frequencies than in stationary populations, a process known as 'gene surfing' (Edmonds *et al.* 2004; Hallatschek and Nelson 2008). Gene surfing is particularly potent if deme (local population) sizes at the edge of the expansion wave are small (Klopfstein *et al.* 2006), and so their prevalence in marine species is currently uncertain. Recently separated large populations, on the other hand, may appear genetically homogenous even in the complete absence of contemporary gene flow (Fig. 2): such scenarios may explain the lack of genetic differentiation even when data from parasites, morphology or life history suggest population subdivision (McQuinn 1997; Abaunza *et al.* 2008).

Genetic methods are most powerful in zones of secondary contact, that is, in areas where previously isolated and genetically differentiated populations come into contact again. For example, Mediterranean anchovies (*Engraulis encrasicolus*, Engraulidae) seem to consist of at least two very divergent clades, whose origin may either be repeated invasions from the Atlantic (Grant 2005) or separate glacial refugia in the Mediterranean and Black Seas (Magoulas *et al.* 1996). In any case, such regions of secondary contact provide excellent opportunities to identify fine-scale genetic differentiation that can be of immediate relevance for fishery management (Bembo *et al.* 1995, 1996a,b). Similar examples of secondary contact zones include the Strait of Gibraltar (Patarnello *et al.* 2007) and the Florida panhandle (Avisé 1992).

Relatively large population sizes, high connectivity among populations and recent colonization of contemporary habitats mean that levels of genetic variability tend to be higher and differentiation lower in marine than in freshwater species (Ward *et al.* 1994; DeWoody and Avisé 2000). In fact, differentiation is often <1% of the total variation detected ($F_{ST} < 0.01$), leading to doubts on the biological relevance of such low values. Indeed, caution in the interpretation of such small values is advisable, as non-random sampling, statistical artefacts and random genetic patchiness may provide a false impression of population structure where none exists (Waples 1998). However, careful sampling design with temporal and spatial replicates, together with appropriate statistical analyses, can confirm the biological reality of weak genetic

population differentiation, which then is a powerful and conservative measure of true population structure (Bentzen 1998).

Population connectivity in marine fishes on a fine scale

The realization of remarkably small-scale genetic structure in marine species generated renewed interest in using genetic markers for the estimation of larval dispersal in marine species. Especially, with the emphasis on MPAs as a tool for marine conservation, the question of realized dispersal of pelagic larvae has found renewed importance, as the function of MPAs in a regional context depends critically on the demographic exchange between the MPA and surrounding areas (Botsford *et al.* 2003; Palumbi 2003). On one extreme, retention of all life-history stages within an MPA negates any positive effects on surrounding areas, while on the other extreme, total export of larvae or juveniles from the MPA may limit the conservation value of the protected area (Palumbi 2003). Some information on realized dispersal from MPAs is therefore required, and although data on adult migration are accumulating (Pittman and McAlpine 2003), little is known about the effect of larval dispersal, which most likely dominates the level of demographic connectivity of protected areas with surrounding regions. Molecular approaches offer a range of approaches that can help estimate larval dispersal and thus small-scale population connectivity (Selkoe *et al.* 2008).

On a fairly simple level, dispersal distances can be estimated from the increase of genetic differentiation with geographic distance (isolation by distance, IBD; Rousset 1997; Palumbi 2003). Available genetic data suggest mean dispersal distances of 10–150 km in many marine invertebrate and fish species (Buonaccorsi *et al.* 2004, 2005; Cunningham *et al.* in press), estimates that are consistent with observations from invasive species (Shanks *et al.* 2003). However, larval durations increase with lower water temperatures (O'Connor *et al.* 2007), and there is evidence that slopes of the IBD decrease and connectivity increases at higher latitudes (Laurel and Bradbury 2006; Kelly and Eernisse 2007). Furthermore, while the assumption of a simple logarithmic distribution of dispersal distances may be valid over the long-term, year-to-year variation in oceanographic conditions results in considerable annual differences in larval dispersal

(Mitarai *et al.* 2008). Integration of genetic data with explicit oceanographic models and other data is therefore necessary for valid estimates of larval dispersal (Cowen *et al.* 2006; Galindo *et al.* 2006; Selkoe *et al.* 2008).

Another approach to investigate fine-scale dispersal in marine species with low genetic population differentiation is parental assignment of larvae and recruits, allowing the identification of recruits originating from local adult fish. The approach is currently used extensively in salmonid populations (Bentzen *et al.* 2001), mainly to estimate reproductive success (Dickerson *et al.* 2002; Seamons *et al.* 2004), interactions between wild and hatchery fish (Araki *et al.* 2007) and the evolution of life-history strategies (Garant *et al.* 2003). Unfortunately, parentage assignment in marine fishes is not trivial: the combination of many unsampled candidate parents with some unavoidable genotyping error reduces the power of analyses (Hauser *et al.* 2007), although new high-throughput markers may improve assignment success (Anderson and Garza 2006). Nevertheless, in combination with other data (Selkoe *et al.* 2008), this approach has already provided astounding estimates of self-recruitment in reef fishes (Jones *et al.* 2005) and may also provide fine-scale estimates of connectivity in temperate species (Hauser *et al.* 2007).

Spatial and temporal scale of adaptation

Paradigm shifts

Although neutral genetic markers have contributed considerably to our understanding of structuring in marine fishes (Carvalho and Hauser 1994; Ward 2002), they do not necessarily convey information on the extent or importance of adaptive variation. It is well established that neutral and adaptive genetic variation are typically uncoupled (Lynch 1996; Reed and Frankham 2001), and that apparent genetic homogeneity revealed by neutral markers such as microsatellites might be underlain by significant heterogeneity in adaptive variation (Larsen *et al.* 2007). The extent and dynamics of local adaptation is the key to understanding the ecological and evolutionary processes that influence biodiversity, as well as providing a spatially explicit framework for the conservation of genetic resources. In consequence, there has been increasing emphasis on the development and application of approaches that more effectively assess the scale of adaptive

processes. The demonstration, for example, that locally self-recruiting populations occur in marine fishes (Jones *et al.* 1999; Cowen *et al.* 2006; Ruzzante *et al.* 2006) has challenged our views on adaptation in the marine environment. Rather than indicating high gene flow that may constrain adaptive differentiation, weak structuring at neutral loci might also derive from typically large population size where differentiation via drift is negligible, as well as historical effects such as recent colonization (Bigg *et al.* 2008). Thus, the conditions of large population size and local recruitment are likely to generate adaptive variation at finer scales, as supported by recent evidence (reviewed by Conover *et al.* 2006; Kochzius in press).

Such local adaptation is highly relevant to fisheries management. It is not merely the conservation of genetic *diversity* (putatively neutral and adaptive diversity at the DNA level), that is critical for ensuring the perpetuation of stocks; it is the preservation of genetic *resources* (diversity at the DNA level and its phenotypic expression at ecologically important traits). For example, although the levels of genetic diversity were similar before and after two population crashes in North Sea cod, temporal genetic data indicated extinction and replacement of a local population (Hutchinson *et al.* 2003). Such demographic change, through a combination of reduced spawning stock biomass and immigration by genetically distinct fishes may thus have altered the range of adaptive potential in North Sea cod. Such a scenario would, however, depend crucially on factors including population size, selection pressures and levels of gene flow. Extirpation of locally adapted assemblages is of particular relevance to a vulnerable species experiencing continued environmental change such as global warming (O'Brien *et al.* 2000). Thus, any focus on adaptation in the wild necessitates an evaluation of putative selective pressures and fitness variation (Endler 2000) – both of which are now convincingly integrated with the application of neutral and selected markers (Larsen *et al.* 2007). Additional insights are afforded by empirical demonstrations of the adaptive nature of obvious traits related to viability and fertility (Rowe *et al.* 2008; Olsen *et al.* 2008).

There are two main time scales on which local adaptation is relevant here: first, in the short term through its effects on local recruitment patterns due to demographic variation (Rowe *et al.* 2008), and second, by affecting long-term population

persistence in relation to population connectivity and resilience to environmental change (Hilborn *et al.* 2003; Olsen *et al.* 2008). It is particularly important to distinguish between population differentiation representing genetic heterogeneity relevant to management strategies, and phenotypic plasticity in response to environmental variation that may not represent local adaptations (Conover *et al.* 2006). Spawning group heterogeneity in Atlantic herring, for example, appears to comprise a mix of essentially phenotypically plastic and locally adapted assemblages (McQuinn 1997; Bekkevold *et al.* 2005; Jørgensen *et al.* 2005), although it was not possible to quantify directly the genetic component of such putatively adaptive variation. Distinguishing between such plasticity and adaptive variation, which by definition has a heritable component, is important in terms of predicting response to environmental change and conservation of genetic resources. Alternative approaches employing common garden experiments or direct analysis of candidate genes can yield some such estimates (Conover *et al.* 2006; Larsen *et al.* 2007).

Thus, there has been a marked shift from descriptive studies that may indicate potential for local adaptation (Hansen *et al.* 2002) to the empirical analysis of ecological traits influencing fitness variation (Larsen *et al.* 2007; Olsen *et al.* 2008). Coincident with the development of markers targeting genes under selection and the exploration of linkages between ecological trait and genetic variation (Giger *et al.* 2008; Naish and Hard 2008) has been the burgeoning of genomic technologies (Goetz and MacKenzie 2008). The generation of large DNA sequence data bases and expressed sequence tags provides the basis for studies on gene expression (Giger *et al.* in press), as well as facilitating a search for candidate genes (Larsen *et al.* 2007). Both such developments afford novel ways for examining adaptive variation in the wild. In addition to classical approaches for detecting local adaptation (Carvalho 1993; Conover *et al.* 2006), innovative methods based on parentage analysis that enable empirical estimates of fitness variation (Neff 2001; Rowe *et al.* 2008), common garden experiments (Marcil *et al.* 2006b; Hutchings *et al.* 2007), and the application of landscape genetics to examine covariance in spatial patterns of environmental and genetic variation (Bekkevold *et al.* 2005; Jørgensen *et al.* 2005; Hemmer-Hansen *et al.* 2007b) have further gen-

erated insights into the dynamics of adaptation in wild fishes.

Spatial scale of adaptive differentiation

In parallel to the discovery of fine-scale population differentiation at neutral markers, even smaller-scale differences at selected markers and phenotypic traits were discovered. Initially, and especially in the allozyme era, such selective effects were considered a complicating nuisance for stock structure analyses (Carvalho and Hauser 1994). More recently, however, the potential implications of adaptive differences have been recognized (Conover *et al.* 2006). Adaptive differentiation at geographic scales smaller than neutral genetic variation was already noted using protein and allozyme variation, and more recently using DNA variation at selected genes (Pogson *et al.* 1995; Hemmer-Hansen *et al.* 2007a), patterns of gene expression (Marchand *et al.* 2006; Larsen *et al.* 2007) and phenotypic traits (Marcil *et al.* 2006a,b; Hutchings *et al.* 2007). In some cases, such selective genetic differentiation can be related to barriers to gene flow (Veliz *et al.* 2006b), or environmental differences (Marchand *et al.* 2003; Jørgensen *et al.* 2008), but in other cases, such correlations are less clear (Hutchings *et al.* 2007). Instead of the isolation by distance patterns commonly observed at neutral markers and caused by limited dispersal within a continuous distribution (Rousset 1997), selected markers show often abrupt genetic discontinuities (Fig. 3, Skarstein *et al.* 2007). Such findings pose the interesting and for management highly relevant question how local adaptation can arise despite presumably high gene flow (Conover *et al.* 2006).

Adaptive divergence arises from the balance between the diversifying effects of selection and the homogenizing effects of gene flow (Garant *et al.* 2007). Therefore, negative relationships between adaptive divergence and gene flow are commonly found in the literature (Räsänen and Hendry 2008). At low levels, gene flow can enhance adaptive divergence by increasing genetic diversity, introducing new beneficial alleles and reducing inbreeding (Garant *et al.* 2007). These effects are particularly pertinent for very small populations, and in relatively large marine populations, gene flow may be primarily a force limiting local adaptation by homogenizing allele frequencies and introducing maladapted genes. However, gene flow

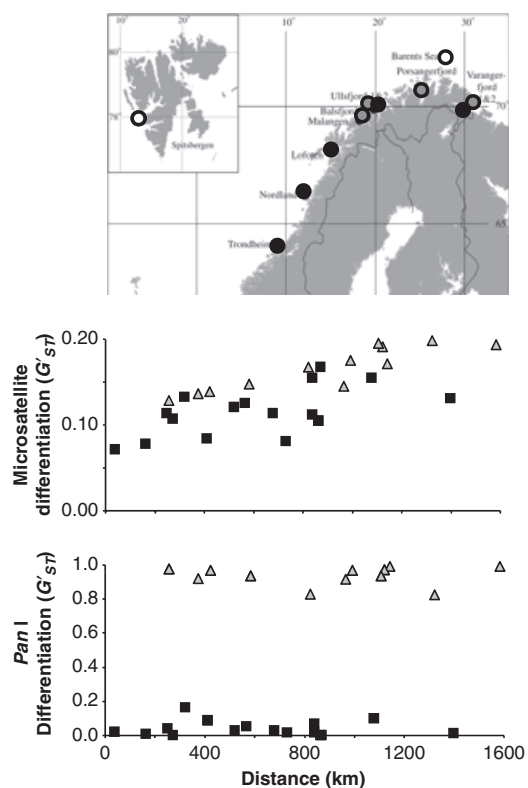


Figure 3 Relationship between pairwise genetic differentiation at putatively neutral microsatellites (top) and *Pan I* (under selection, bottom) with geographic distance in Norwegian cod. Two groups are distinguished in the map: the North-east Arctic cod (white circles) and the Norwegian coastal cod (full circles), which can co-occur within the same fjords. Grey circles are ambiguous samples potentially including fish from both groups – these samples were excluded here. Open triangles are comparisons between groups; filled squares are comparisons within groups. Genetic differentiation is measured as G'_{ST} , a multiallele estimator of F_{ST} corrected for within-population diversity (Hedrick 2005b). Note that microsatellites show a tight isolation-by-distance relationship, whereas *Pan I* differentiation is high among groups irrespective of distance. Data and map from Skarstein *et al.* (2007).

can cause adaptive divergence if dispersal is not random with respect to habitat and phenotype. For example, with higher dispersal of lake-type sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae) into a lake outlet than the lake inlet, adaptive divergence between lake and outlet sticklebacks is reduced, but that between inlet and outlet populations may be increased (Moore and Hendry 2005; Moore *et al.* 2007). Such effects may be common in marine species, where dispersal in unidirectional currents

may constrain adaptive divergence in populations downstream (Veliz *et al.* 2006b; Pringle and Wares 2007), but not elsewhere.

The reverse causal pathway is also possible, and adaptive divergence may constrain gene flow by selection against immigrants and hybrids, so-called reinforcement of adaptive divergence (Garant *et al.* 2007), potentially leading to ecological speciation (Rocha and Bowen 2008). Such selection against migrants and hybrids is well-known in hybridization between species (Hatfield and Schluter 1999; Gilg and Hilbish 2003; Garrett *et al.* 2007), but also between isolated populations of the same species, for example, in the contact zone between North Sea and Baltic cod (Nielsen *et al.* 2003).

The causality of gene flow – adaptive divergence relationship is of considerable practical importance. If gene flow does indeed restrict adaptive divergence, standard approaches using neutral genetic markers and landscape genetic approaches may be sufficient to obtain at least a rough estimate of adaptive variation, as long as estimates of molecular divergence do indeed reflect gene flow. If, on the other hand, adaptive divergence limits gene flow, genetic population structure may be less predictable from larval dispersal patterns, and may be more related to environmental factors that are sometimes obvious (Jorgensen *et al.* 2008), but sometimes not. Furthermore, the implications for recruitment dynamics may be considerable – for example, occasional episodes of high influx of larvae from divergent populations may be of little benefit to local recruitment and may indeed be detrimental by increasing maladaptive traits in the population (migration load). In this case, selective mortality may be an important factor in determining population isolation – reports of such selective mortality in recruits to local populations (Planes and Lenfant 2002; Veliz *et al.* 2006b; Vigliola *et al.* 2007) lend considerable support to this idea.

More pragmatically, local adaptation may provide powerful markers for stock identification. For example, genetic differentiation among Atlantic cod collected around Iceland was two orders of magnitude higher in the selected *Pan I* locus ($F_{ST} = 0.261$) than at nine microsatellites ($F_{ST} = 0.003$) (Pampoulie *et al.* 2006). Similarly, walleye pollock (*Theragra chalcogramma*, Gadidae) populations in the north Pacific Ocean and Bering Sea, which were weakly structured at 14 microsatellite loci (global $F_{ST} = 0.002$, $P < 0.001$; O'Reilly *et al.* 2004), showed an order of magnitude higher estimates of

population differentiation at the *Pan I* locus (global $F_{ST} = 0.036$, $P < 0.001$; Canino *et al.* 2005). In European flounder (*Platichthys flesus*, Pleuronectidae), differentiation at a heat shock protein gene between the Baltic and North Seas was more than an order of magnitude higher than that of neutral microsatellites (Hemmer-Hansen *et al.* 2007a). Such selected markers can be used to increase the power of assignment tests (Hauser *et al.* 2006) and mixed stock analyses (Ruzzante *et al.* 2000a), an approach that is already extensively used on sockeye salmon (*Oncorhynchus nerka*, Salmonidae) in Alaska (Smith *et al.* 2005, 2007), although the interpretation of genetic differentiation in terms of gene flow is more complex.

Genetic differentiation at selected markers is caused by both selection and limited gene flow, and it can be difficult to disentangle the two forces. In one way, genes under selection may be useful markers for the detection of adaptive divergence between populations. Indeed, the case has been made recently that selected genetic markers should be used to determine a 'population adaptive index' as a measure of adaptive genetic diversity and a basis for conservation prioritization (Bonin *et al.* 2007). However, fisheries management is typically interested in the identification of demographically independent units (Carvalho and Hauser 1994; Waples *et al.* 2008) and the definition of stock boundaries representing restricted connectivity. Differences at selected markers, on the other hand, may be due to weak selection with limited dispersal or strong selection with extensive dispersal. Ideally, selection could be measured by common garden (Hutchings *et al.* 2007) or transplant experiments (Case *et al.* 2006), although this is seldom possible in marine species. An alternative approach is to assume a reasonable range of selection differentials to derive a range of likely dispersal distances. Such use of selected markers for the estimation of gene flow is commonplace in the hybrid zone literature (Barton and Hewitt 1985), and has been recently extended to intraspecific genetic clines expected from selected markers (Laurent *et al.* 2006; Sotka and Palumbi 2006). Another, potentially more widely applicable approach exploits covariation between different selected markers by estimating linkage disequilibrium between loci (non-random association of alleles at different loci; Lenormand *et al.* 1998; Nielsen *et al.* 2003; Sotka and Palumbi 2006). Clearly, such approaches need

several selected markers and thus have been rarely applied in marine fishes so far. However, a recent genome-wide population survey of Atlantic cod along the Norwegian coast revealed 29 loci that were clearly under directional selection and showed relatively high F_{ST} values between 0.08 and 0.83 (Moen *et al.* 2008). While the direct interpretation of this differentiation in terms of limited dispersal is not warranted, some of the above applications may provide useful insights into the biology and life history of marine species (Nielsen *et al.* 2005). However, for studies employing selected markers, the collection of adequately fine-scale temporal and spatial samples (Waples 1998) is probably even more important than when presumably neutral loci are employed.

Temporal scale of adaptive differentiation

In addition to clear evidence that marine fishes may exhibit adaptive variation across small spatial scales is the associated finding that some populations may exhibit rapid genetic change (Conover *et al.* 2006). In fact, selection may be sufficiently strong during the larval or juvenile phase to produce adaptive divergence within a single generation. Such selective mortality during the lifetime of individual cohorts has been reported not only for allozyme loci (Lenfant and Planes 2002; Veliz *et al.* 2006b), but also for mtDNA (Vigliola *et al.* 2007). Furthermore, differences in growth or fecundity (Case *et al.* 2006) may also result in very rapid adaptive differentiation (Case *et al.* 2005). In such cases, careful and fine-scale spatial and temporal sampling is required for a sound interpretation of data. Although such data are complicated to interpret in terms of stock structure, they can provide powerful insights into the life history of otherwise untraceable species. For example, genetic differentiation between juveniles in nursery areas of an essentially panmictic population of common sole (*Solea solea*, Soleidae) allowed the development of a testable model postulating selection in nursery areas. Such processes led to genetically differentiated adults and potentially biased survival of different genotypes in the nursery areas in subsequent generations (Guinand *et al.* 2008).

Given this potential speed of adaptation, concerns about adaptive responses in life-history characters to exploitation are warranted. Decreases in age and size at maturity are common in

exploited species (Trippel 1995; Law 2000), and given the importance of life-history traits as key determinants of population dynamics, such changes will have direct impacts on stock biomass, demography and economic yield (Law 2000), with associated effects on predator–prey dynamics, competitive interactions, relative species abundances and other ecological relationships. In general, such phenotypic changes result from both phenotypic and genetic responses. However, the extent of genetic change may determine the reversibility of phenotypic shifts (Law 2000; de Roos *et al.* 2006; but see also Edeline *et al.* 2007) and the scope for population recovery (Walsh *et al.* 2006), and has thus attracted considerable interest (Jorgensen *et al.* 2007). The direction of observed phenotypic changes is predicted by life-history evolution (Policansky 1993; Law 2000), and genetic changes have been demonstrated in wild (Reznick and Ghalambor 2005) and laboratory (Conover and Munch 2002) populations of model species. However, evidence from marine exploited species is still scant and equivocal, because it is difficult to separate environmental effects, phenotypic plasticity and genetic changes (Kuparinen and Merilä 2007; Hard *et al.* 2008; Hendry *et al.* 2008; Naish and Hard 2008). In particular, the probabilistic reaction norm approach (Heino *et al.* 2002; Dieckmann and Heino 2007) has been widely publicized as a means to detect genetic change (Jorgensen *et al.* 2007) and even to predict imminent stock collapse (Olsen *et al.* 2004), but has been criticized because environmental and genetic effects cannot be fully separated (Kraak 2007; Kuparinen and Merilä 2007; Law 2007; Browman *et al.* 2008; Hard *et al.* 2008) and because alternative interpretations are possible (Marshall and McAdam 2007). It is also notable that few studies have estimated selection differentials imposed by fishing, with most estimates from Atlantic cod (Law and Rowell 1993; Law 2000; Sinclair *et al.* 2002), plaice (*Pleuronectes platessa*, Pleuronectidae, Rijnsdorp 1993) or Pacific salmonids (Hard *et al.* 2008). Selection differentials in wild populations may be considerably less than assumed in experiments (e.g. Conover and Munch 2002) and models: for example, evolutionary effect at least on growth rates may be limited (Hilborn and Minte-Vera *in press*). Nevertheless, the topic is of considerable relevance to fisheries management and further research is urgently required.

Population size in marine fishes

Paradigm shift

Exploited marine species are commonly distributed over large geographic areas and, as a prerequisite of their commercial importance, have large population sizes. The perception that many marine populations are inexhaustible has changed considerably, based on high-profile fishery collapses and highlighting the vulnerability of many marine stocks. Nevertheless, complete extinctions are rare (Dulvy *et al.* 2003), and the number of fish even in commercially collapsed stocks tends to remain large (Myers *et al.* 1997). Some recent listings of marine species on the IUCN Red List [e.g. Atlantic cod, Atlantic halibut (*Hippoglossus hippoglossus*, Pleuronectidae), dogfish (*Squalus acanthias*, Squalidae)] were precipitated by large declines in biomass rather than by small population sizes, triggering a controversy about true extinction risks in those species (Dulvy *et al.* 2005). Indeed, most exploited marine species apparently never reach sufficiently small population sizes for concerns about the viability, inbreeding, stochastic genetic changes or loss of genetic diversity (Ryman *et al.* 1995), all of which are major concerns in many terrestrial and freshwater populations.

However, several recent papers suggested that, from a genetic viewpoint, the large number of fish in the sea may be misleading and that the genetically effective size (N_e) of marine species may be remarkably small (Table 1). The effective population size can be defined as the size of an ideal population with the same rates of genetic change as the observed one, and thus provides information on evolutionary change as well as ecological differences between observed and ideal populations. Low N_e values may not only have important implications for the conservation and management of marine fishes, but may also allow considerable insights in the population ecology, evolution and scope for adaptation. They certainly demonstrate our limited understanding of demographic processes in marine populations.

Biological mechanisms leading to low N_e/N ratios

Studies reporting N_e estimates from marine species (Table 1) allow three important observations:

1. With very few exceptions, N_e ranges from the 100s and low 1000s, and is thus within the range where loss of genetic variability due to genetic drift may occur (Frankham *et al.* 2002).

Table 1 Estimates of effective population sizes in marine species, with location of the study, number of loci used, \hat{N}_e estimates and confidence limits and the \hat{N}_e/\hat{N} ratio.

	Species	Location	Loci	\hat{N}_e	Confidence limits	\hat{N}_e/\hat{N}	Reference
Atlantic cod	<i>Gadus morhua</i> Gadidae	NE England	3	121 ¹	51–426	4×10^{-5}	Hutchinson <i>et al.</i> (2003)
Atlantic cod	<i>G. morhua</i>	Baltic Sea, Moray Firth	9	844 ¹ 1193 ² 1068 ¹ 2067 ²	428–2353 ¹ 605–4680 ² 423– ∞ ¹ 651– ∞ ²	n/a	Poulsen <i>et al.</i> (2006)
Darkblotch rockfish	<i>Sebastes crameri</i> , Sebastidae	Oregon	7	9157 ^{1c}	6495–12 215	4×10^{-4}	Gomez-Uchida and Banks (2006)
Red drum	<i>Sciaenops ocellatus</i> , Sciaenidae	Gulf of Mexico	8	2365 ^{1c} 3516 ^{2c} 1853 ⁴	833– ∞ ^{1c} 1785–18 148 ^{2c} 317–7226 ⁴	10^{-3}	Turner <i>et al.</i> (2002)
Red drum	<i>S. ocellatus</i> , Sciaenidae	SW Atlantic	5	560 ^{1c}	395–748	n/a	Chapman <i>et al.</i> (2002)
Plaice	<i>Pleuronectes platessa</i> , Pleuronectidae	Iceland North Sea	8	1733 ² 19 535 ²	1063–3598 3435–70 000	2×10^{-5}	Hoarau <i>et al.</i> (2005)
Red snapper	<i>Lutjanus campechanus</i> , Lutjanidae	Texas Alabama Louisiana	19	1098 ^{2c} 1235 ^{2c} >75 000 ^{2c}	652–2706 777–2515 >75 000	10^{-3}	Saillant and Gold (2006)
Gag grouper	<i>Mycteroperca microlepi</i> , Serranidae	Florida	11	30 975 ⁴	22 750–38 100	10^{-2}	Jue (2006)
New Zealand snapper	<i>Pagrus auratus</i> , Sparidae	Tasman Bay, NZ	6	176 ¹	80–720	2×10^{-5}	Hauser <i>et al.</i> (2002)
Tiger prawn	<i>Penaeus esculentus</i> , Penaeidae	Moreton Bay, AUS	8	797 ¹ 1013 ² 1165 ³	366–4182 580–2888 700–2950	10^{-3}	Ovenden <i>et al.</i> (2007) ⁱ
European flat oyster	<i>Ostrea edulis</i> , Ostreidae	Sète, France	4	11.4 ^{B1} 27.5 ^{B5} 19.7 ^{B6}	8–15.8 24.1–31.3 10.3–368.3	n/a	Hedgecock <i>et al.</i> (2007)
Striped bass	<i>Morone saxatilis</i> , Moronidae	South Carolina	3 RFLP	30 ^{1c}	2–609	3×10^{-4}	Diaz <i>et al.</i> (2000)
Atlantic cod	<i>G. morhua</i>	Atlantic	1 mt	1622–432k ⁴		10^{-5} – 10^{-6}	Arnason (2004)
White sea breem	<i>Diplodus sargus</i> , Sparidae	Banyuls Bay, France	17 A	793 ¹	420–7153	n/a	Lenfant and Planes (2002)
Sardine	<i>Sardina pilchardus</i> , Clupeidae	Bay of Biscay	27 A	232 ¹ 596 ²	119–475 ¹ 397–967 ²	10^{-8} ⁱⁱ	Laurent and Planes (2007) ⁱ

Notes: RFLP, restriction fragment length polymorphism; A, allozymes; mt, mtDNA.

¹Temporal moment based (Waples 1989).

²Temporal pseudo-maximum likelihood (Wang 2001).

³Temporal maximum likelihood (Anderson *et al.* 2000).

⁴Coalescence (Beerli and Felsenstein 2001).

⁵Linkage disequilibrium (Waples 1991).

⁶Heterozygote excess (Pudovkin *et al.* 1996).

^cCorrection for overlapping generations (Jorde and Ryman 1995).

^BNumber of breeders.

ⁱOnly 1 of 2 years considered – results for second year are comparable.

ⁱⁱ \hat{N}_e/N estimated from biomass and weights in Somarakis *et al.* (2006).

Unless specified otherwise, all studies employed microsatellite markers. Studies using equilibrium estimates of \hat{N}_e from genetic diversity are not considered.

2. Estimates of effective population size in marine fishes are between two and five orders of magnitude smaller than census population sizes

(mean N_e/N ratio: $10^{-3.99}$), and are thus orders of magnitude lower than those reported for most other species (Frankham 1995).

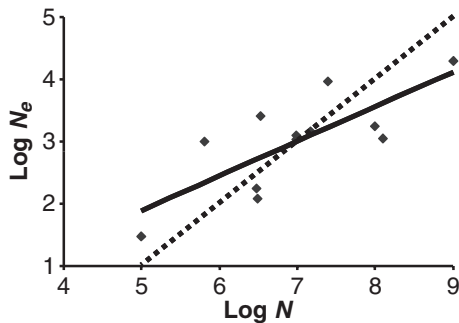


Figure 4 Relationship between \hat{N}_e and population size in marine species listed in Table 1 (microsatellite data only). $\text{Log } \hat{N}_e$ increases with $\text{log } \hat{N}$ (linear regression, $r^2 = 0.59$, $P = 0.0034$), but the slope of the regression (solid line) is significantly smaller than 1 (t -test, $P = 0.013$; $\Delta\text{AIC} = 7.8$), indicating that N_e/N ratio is smaller in larger populations. The dotted line shows the expectation for a constant N_e/N ratio of 10^{-4} , the average of all studies.

- N_e is positively correlated with N , but the relationship is significantly better explained by a power function ($N_e = 0.1274N^{0.5574}$) than a linear function ($\Delta\text{likelihood} = 3.9$, $P = 0.005$; $\Delta\text{AIC} = 4.29$). When plotting $\text{log } N_e$ against $\text{log } N$, the linear relationship has a slope that is significantly smaller than 1 expected from a constant N_e/N ratio (Fig. 4). In other words, the N_e/N ratio decreases with increasing population size.

The large discrepancy between estimates of N_e and census population size may be due at least in part to publication bias: most marine populations are large (at least millions of individuals), and with generally manageable samples sizes, finite estimates of N_e are difficult to obtain for very large populations (Ovenden *et al.* 2007). Furthermore, most estimates are from demersal and benthic species with pelagic larvae, possibly because such species may show more pronounced population structure than pelagic species (Hauser and Ward 1998), thus providing relatively small isolated populations in bays and estuaries. Although studies reporting low N_e/N ratios are accumulating and are remarkably consistent in their findings, there have been challenges to the validity of such estimates (Flowers *et al.* 2002; Poulsen *et al.* 2006). Immigration (Wang and Whitlock 2003) and sampling biases (Waples and Yokota 2007), as well as some other factors such as selection, may cause a downward bias of N_e estimates in marine species, though most authors explicitly address such artefacts. Such factors are unlikely to explain several orders of magnitude

discrepancy between N_e and census population size, and studies to date (Table 1) provide strong evidence that extremely small N_e/N ratios do indeed occur in marine species. What are the possible biological mechanisms for such extreme reductions in N_e ?

Some of the often cited causes of low N_e/N ratios, such as fluctuations in population size and populations not in mutation-drift equilibrium, only concern long-term estimates of N_e . Estimates from temporal samples, linkage disequilibrium and heterozygote excess apply to the time between samples or a few generations before the sample was taken (Waples 2005), and so longer-term factors appear less important. While population size fluctuations may affect N_e in the shorter term, such population bottlenecks are usually known because of the short time scale of estimates. In any case, a comparison between long-term (e.g. coalescence) and short-term (e.g. temporal) estimates of N_e may provide valuable insights into the long-term demographic history of a population (Beerli *in press*).

Deviation from a sex ratio of 1:1 can cause a reduction of N_e relative to census size (Nunney 1993). Observed sex ratio may here be not relevant, as behaviour may change sex ratios of individuals ready to mate (Kvarnemo and Ahnesjö 1996). Indeed, behavioural studies suggest that Atlantic cod males may establish hierarchies determining access to females, which may cause higher variance in reproductive success in males, affect operational sex ratios and lower effective population size (Bekkevold *et al.* 2002; Rowe *et al.* 2008). However, extreme biases in sex ratios would be required to explain N_e several orders of magnitude smaller than N – for example, to reduce N_e by only one order of magnitude ($N_e/N = 0.1$), one of the sexes would have to constitute 97.4% of the spawning population. Biased sex ratios may therefore contribute to low effective population size, but they are unlikely to be a major factor.

The most likely and most important factor reducing N_e in marine species is high variance in reproductive success among individuals. An ideal population, where $N_e = N$, assumes random reproductive success – a higher variance in family size would reduce N_e to numbers lower than N . However, in marine species, with their high fecundity and high mortality during the pelagic larval phase (type III survivorship), survival may not be random, but dependent on time and place of spawning and hatching ('match–mismatch hypothesis,' Cushing 1990). Especially in species where spawning occurs

in a single batch, local environmental conditions may lead to random 'sweepstake recruitment' events (Hedgcock 1994), where entire families either survive or die. Complete family-specific mortality leads to a reduction in N_e/N ratio that is proportional to survival during the family-specific mortality phase (Waples 2002). Data available so far suggest that the scope for sweepstake recruitment may be higher in larger populations, as the N_e/N ratio is lower in larger populations. Similar observations have been reported previously in the flower beetle *Tribolium castaneum* (Tenebrionidae, Pray *et al.* 1996) and in salmonid fishes (Palstra and Ruzzante 2008). In addition, relatively small Atlantic cod populations in Arctic marine lakes have N_e/N ratios orders of magnitude higher than reported for this species elsewhere (Hardie *et al.* 2006).

Sweepstake recruitment allows for some predictions independent of N_e estimates (Hedgcock 1994). For example, as larvae originate from relatively few spawners, there should be lower diversity within, and higher differentiation among, larval cohorts than samples of adults. This prediction that has been verified in some marine species (Planes and Lenfant 2002; Selkoe *et al.* 2006; Burford and Larson 2007; Laurent and Planes 2007) but not in others (Flowers *et al.* 2002; Gilbert-Horvath *et al.* 2006). Furthermore, larvae or juveniles in recruiting batches may be related (Planes *et al.* 2002), although such related-

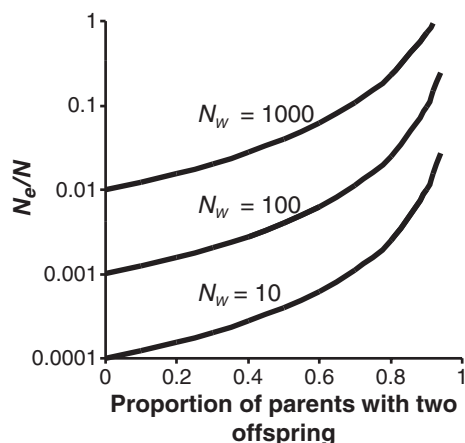


Figure 5 N_e/N ratios as a function of the proportion of successful spawners in a population of 100 000 individuals. The proportion of parents with two offspring each is shown on the X-axis, with 10, 100 or 1000 'sweepstake winners' (N_w) sharing the rest of the recruitment. Note that N_e/N ratios are low even if a relatively large proportion of the population achieves replacement reproductive success. Calculated using Equation 6c in Hedrick (2005a).

ness is not always detectable (Herbinger *et al.* 1997). Indeed, despite the potential for extensive mixture, many marine species may disperse as groups of related individuals (Veliz *et al.* 2006a), thus providing the opportunity for family-specific mortality.

Even assuming extensive sweepstake recruitment, low N_e/N ratios may be puzzling, given that the N_e depends on lifetime, not the annual, reproductive success. In long-lived species spawning in several batches per year (most species in Table 1), one would therefore have to argue that there are consistent lifetime winners and losers in the sweepstakes. However, N_e is not equivalent to the number of successful breeders in the population. N_e/N ratios are primarily affected by the small proportion of winners, and are surprisingly robust to a relatively large proportion of parents with two offspring¹ (Hedrick 2005a; Fig. 5). For example, if in a population of 100 000 fish, half of the parents (50 000 individuals) produce two offspring each, 49 900 no offspring at all and the remaining 100 an equal share of the remaining recruitment (1000 offspring each), the N_e/N ratio would be 0.004, even though more than half the population was reproductively successful (Hedrick 2005a). Such a bias in reproductive success with many losers, many average spawners and very few extremely successful parents is possible even in long-lived fish. Many long-lived demersal fishes have a high variance in annual recruitment success, with few highly abundant year classes (Hamer and Jenkins 2004; Sakuma *et al.* 2006), suggesting that opportunities to become a 'sweepstake winner' may be limited. Furthermore, annual and, more importantly, lifetime reproductive success in species with indeterminate growth depends strongly on age, as older large females produce not only more (Cuellar *et al.* 1996; Zeldis and Francis 1998), but also potentially more viable eggs and larvae (Berkeley *et al.* 2004; Fisher *et al.* 2007; Sogard *et al.* 2008). Therefore, only older spawners ready in years of excellent recruitment may have a chance to become rare 'sweepstake winners.'

In addition to such temporal considerations, spatial variation may be an important contributor to low N_e/N ratios. Many of the species in Table 1 are relatively sedentary as adults (e.g. Willis *et al.* 2001), even though they exchange recruits via larval dispersal – adult habitats are therefore

¹Two offspring per parent are required in a stable population, because in sexual species, each offspring has two parents.

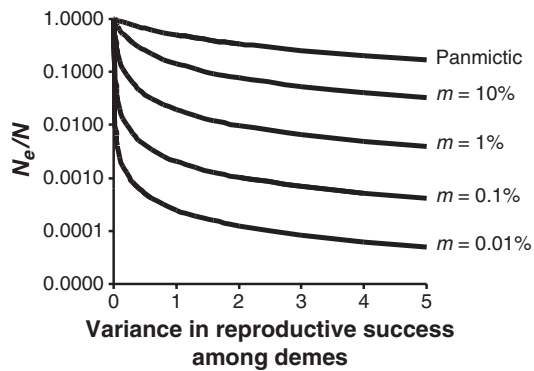


Figure 6 Effect of variance in mean reproductive success among demes and migration rates (m) on N_e/N ratios. For comparison, if only 2 out of 10 equally sized demes were reproductively successful and the other eight did not produce any offspring, the variance in reproductive success would be about 4.4. Calculated using Equation 25 in Nunney (1999), assuming random reproductive success among individuals and no inbreeding within demes.

temporary islands within a panmictic population (Nunney 1999). If such adult habitats vary in productivity, for example, by the quality of nursery grounds for larvae downstream of the habitat, N_e/N ratios may be an order of magnitude lower than expected from variance in individual reproductive success alone (Nunney 1999; Fig. 6). The effect is further increased if subpopulations are relatively isolated (i.e. are connected by low migration rates). Turner *et al.* (2002) cited differences in productivity among isolated subpopulations as the primary reason for the low N_e/N ratio in red drum in the Gulf of Mexico. Interestingly, the negative relationship between gene flow and adaptation may further increase the imbalance in productivity between populations (Garant *et al.* 2007) – high migration rates from a source to a sink population may cause a large influx of maladapted migrants into the sink, thus reducing its productivity and further increasing differences in productivity.

The reduction in N_e compared to population size is usually seen as a demographic process not involving genetic differences among spawners. However, selection could reduce N_e if conditions favour offspring from specific families. Indeed, there is evidence for genotype-specific survival in both captive (Mork and Sundnes 1985a; Geiger *et al.* 2007; Moyer *et al.* 2007) and wild populations (David and Jarne 1997; Planes and Romans 2004). Given the low power of such experiments, this phenomenon might be more common than gener-

ally assumed. Furthermore, selection caused by recessive deleterious mutations may be an important factor in highly fecund species, where many cell divisions in the germline necessary to produce millions of eggs and billions of sperm may provide the potential for high per-generation mutation rates and thus for the accumulation of such mutations as genetic load (Launey and Hedgecock 2001). In oysters (*Crassostrea gigas*, Ostreidae), the first species where low N_e/N ratios were reported (Hedgecock *et al.* 1992), high family-specific mortality is a result of such genetic load causing inbreeding depression if expressed in crosses among similar genotypes (Launey and Hedgecock 2001). In many species, specific families might therefore be doomed by a lethal combination of many such recessive mutations. This inbreeding effect is possible even in crosses among relatively distant relatives and can be exacerbated by stressful environmental conditions (Camara *et al.* 2008). Although such inbreeding effects have not been reported in marine fishes, they might help explain extremely low N_e in some species (Hedgecock, D. pers. comm.). Furthermore, expression of genetic load after a population size reduction might contribute to long recovery times after fishery collapses, which are directly proportional to the severity of the collapse (Hutchings and Reynolds 2004).

Implications and significance of small effective population sizes

Small effective population sizes in marine populations are interesting scientifically, but potentially have also important implications for our understanding of the demographic and evolutionary dynamics of marine species, which in turn may affect management goals and measures.

In evolutionary genetic terms, small N_e has important effects on the potential for adaptation and speciation in marine species. Most empirical estimates of N_e in marine species range from the hundreds to the low thousands (Table 1). Although such values may not be typical for marine population in general, they do demonstrate that some populations with large census sizes can be sufficiently small in evolutionary terms that they are at risk from deleterious effects of inbreeding (Hoarau *et al.* 2005) and genetic drift. In New Zealand snapper (*Pagrus auratus*, Sparidae), for example, Hauser *et al.* (2002) detected a significant decrease in microsatellite variability related to small N_e in an

overexploited population. Because of the complex relationship between molecular and quantitative genetic variation (Naish and Hard 2008), the conservation implications of such reduced microsatellite diversity are uncertain. Nevertheless, loss of even putatively neutral genetic variation may pose a threat for the long-term adaptive potential of a population under changing environmental conditions. A loss of alleles at neutral and weakly selected genes may not contribute much to extant quantitative genetic variation, but may be potentially adaptive in different environments (Ryman *et al.* 1995). On the other hand, genetic variability even in relatively isolated populations may be replenished by immigration over the longer term. However, as previously emphasized, replenishment of individuals and genetic diversity may not necessarily represent the persistence of a locally adapted population. In any case, such considerations are imperative in the face of major global pressures on marine systems, including climate change and shifts in ecosystem functioning.

In practical terms, the low N_e/N ratios may be the reason for our ability to identify at least some marine populations by their allele frequencies. With a powerful suite of microsatellite markers and sample sizes commonly used in studies of marine fish, F_{ST} values of about 0.002 are statistically distinguishable from zero, thus demonstrating the existence of partially isolated populations. Clearly, when F_{ST} values are so small, it will be necessary to confirm their biological reality by establishing their temporal stability. The time it takes to reach that $F_{ST} = 0.002$ at neutral loci is proportional to population size (Fig. 2): in populations with an N_e of 10 000, this level of F_{ST} is achieved after only 40 generations of complete isolation – somewhat more if migration rates exceed 0.001. In a population of an N_e of one million, this level of F_{ST} would only be achieved after 4000 generations, even with complete isolation; at $N_e = 10$ million it would be about 40 000 generations. If N_e in marine populations was indeed as large as census population sizes, small-scale genetic heterogeneity, such as in Atlantic cod (Ruzzante *et al.* 2000b; Hutchinson *et al.* 2001) or New Zealand snapper (Bernal-Ramirez *et al.* 2003), could never have accumulated in the 10 000–15 000 years since recolonization of high-latitude habitats after the last glaciation. Of course, secondary contact after isolation in glacial refugia may cause genetic differentiation even in large populations, but the ubiquity of genetic differentia-

tion in marine fishes suggests fairly small effective population sizes. In addition, isolation by distance patterns in many marine species are only explainable with N_e that is orders of magnitude smaller than census population sizes unless larval dispersal distances are assumed to be unrealistically small (<1 km; Buonaccorsi *et al.* 2002, 2004, 2005; Gomez-Uchida and Banks 2005; Cunningham *et al.* in press).

The ecological implications of small N_e/N ratios may be even more important for fisheries management. The idea of only relatively few spawners contributing most of the recruitment has immediate appeal to fisheries management, because it could mean that all other fish could be removed without detrimental effect to recruitment. Such a notion is a dangerous one, as it is impossible to predict which fish will be the successful spawners. In fact, it seems likely that successful spawners tend to be older and larger fish (Berkeley *et al.* 2004), thus supporting the view that maintenance of age-structure of exploited species is an important management consideration (Birkeland and Dayton 2005). However, generally weak correlations between spawning stock biomass and recruitment (Cowan and Shaw 2002) may at least in part be caused by a disassociation between population size and the number of successful spawners.

Of more immediate interest is the possibility that low N_e/N ratios are caused by differences in productivity among habitats or subpopulations. Modelling studies confirm the intuitive idea that MPAs are most effective in productive areas (source populations), while locating MPAs in less productive populations maintained by the influx of immigrants (sink populations) may actually harm the overall yield (Crowder *et al.* 2000). Research to investigate the temporal stability of such habitat quality and population productivity difference (Sanford and Menge 2007), its effect on metapopulation dynamics and N_e/N ratios are therefore required. The effect of habitat quality on the level of larval production and metapopulation dynamics could then be confirmed by assessing directional gene flow using genetic markers based on assignment tests (Weetman *et al.* 2006) or coalescence (Marko *et al.* 2007) or by oceanographic modelling (Bode *et al.* 2006; Selkoe *et al.* 2008). It is crucial to view low N_e/N ratios not only as interesting but irrelevant oddities, but also as an important piece in the puzzle of the population dynamics of exploited species.

Atlantic cod as a case study for the paradigm shifts

The challenges and advances in detecting structuring in marine fishes are well illustrated by taking Atlantic cod, *Gadus morhua*, as a case study. Atlantic cod is among the most intensively studied marine fishes, and delineation of Atlantic cod stocks with molecular markers has been underway for more than four decades (Wirgin and Waldman 2005). Several features render its biology typical of other gadoids and demersal fishes of commercial importance: first, cod have historically large census populations, although isolated populations exist and there have been several well-documented population crashes (Wirgin and Waldman 2005); second, dispersal potential is high, based on an extended pelagic larval phase and extensive adult migrations (Robichaud and Rose 2004); third, relatively recent colonization since the Pleistocene in some regions of species' range (Bigg *et al.* 2008) limits the opportunity for accumulation of mutational divergence among populations. Thus, several biological and historical features would be expected to minimize opportunities for genetic structuring—a situation common to many other marine teleosts.

It has long been known that significant genetic differences can be found in cod across the Atlantic (Arnason 2004; O'Leary *et al.* 2007), but evidence for regional genetic structuring was equivocal based on allozymes (Mork *et al.* 1985; Pogson *et al.* 1995) and mitochondrial DNA analyses (Smith *et al.* 1989; Carr *et al.* 1995). Only with the advent of microsatellites, and the targeting of samples during the period of maximum stock integrity (that is, during spawning), has significant genetic divergence been detectable across small spatial scales (Ruzzante *et al.* 2000b; Hutchinson *et al.* 2001). Within the NW Atlantic, for example, microsatellite genetic differentiation has been observed at continental shelf scales for most of the major spawning populations (Ruzzante *et al.* 1998; Beacham *et al.* 2002a). In general, isolated populations were found in association with oceanic gyres promoting the retention of eggs and juveniles. In the Northeast Atlantic, microsatellites revealed significant differentiation among the major cod populations, e.g. North Sea, Baltic Sea and Northeast Arctic cod (Hutchinson *et al.* 2001; Nielsen *et al.* 2003), and these patterns are temporally stable (Poulsen *et al.* 2006). Levels of genetic differentiation among major populations proved to be so high that almost

unambiguous population assignment of individuals is possible (Nielsen *et al.* 2001). Additionally, population structure has been inferred on a much smaller geographical scale. Knutsen *et al.* (2003) found small but highly significant differentiation across a continuous coastal region of just 300 km, demonstrating genetic differentiation in the absence of physical barriers or great distance. Nielsen *et al.* (2003) also found significant genetic differentiation on a small geographical scale, which could be ascribed to a hybrid zone between North Sea and Baltic Sea cod. Even smaller-scale differentiation between populations separated by depth was discovered in Iceland (Pampoulie *et al.* 2006) and in Norwegian fjords (Karlsson and Mork 2003).

Atlantic cod also shows clearly the effects of phylogeographic history in patterns of genetic diversity: for example, there is evidence that the generally weak (though detectable) genetic differentiation between cod populations is at least in part due to a recent colonization of contemporary habitats after the last glaciation (Pampoulie *et al.* 2008a). Furthermore, strong clines at the *Pan I* locus, although maintained by strong selection (Case *et al.* 2006), may have arisen due to secondary contact of previously isolated populations (Case *et al.* 2005). Such an interpretation is supported by historical imprints in microsatellite data in samples from that region (Pampoulie *et al.* 2008b).

Evidence from genetic markers, such as haemoglobin (Sick 1965) and *Pan I* (Pogson 2001), generally support the idea that populations that are weakly differentiated at neutral markers can display stronger genetic differentiation for markers under selection, suggesting that these populations are locally adapted to specific environmental conditions (Fig. 3, Skarstein *et al.* 2007). Differentiation between cod in the North Sea and those in the Barents Sea is moderate at microsatellite loci ($F_{ST} = 0.05$; Hutchinson *et al.* 2001), but nearly fixed differences (different alleles present in the two populations) are found at *Pan I* (Case *et al.* 2005). On a more local scale, microsatellites under selection differentiated inshore and offshore populations in northern Norway (Westgaard and Fevolden 2007). *Pan I* showed almost fixed differences between cod within and between Norwegian fjords (Fevolden and Pogson 1997), possibly related to salinity and temperature (Case *et al.* 2005), although other factors may be important as well (Karlsson and Mork 2003). In any case, evidence from transplant experiments of cod from central to

southern Norway suggests that selective pressures are relatively weak and that the observed differentiation may be due to limited dispersal between isolated populations exposed to different selection pressures over many generations (Case *et al.* 2006).

The biological importance of genetic population structure in cod was illustrated by differences in egg buoyancy and sperm mobility between Belt Sea and Baltic Sea cod (Nissling and Westin 1997). Furthermore, common garden experiments demonstrated differences in body shape (Marcil *et al.* 2006b) and life history (Hutchings *et al.* 2007) between two Canadian cod populations that were only weakly differentiated by microsatellites. In other instances, there is evidence that adaptive divergence limits dispersal, leading to the formation of a hybrid zone in the Western Baltic (Nielsen *et al.* 2003). Such ecological diversity, or 'biocomplexity,' including intraspecific diversity in fitness-related traits such as patterns of migration, maturation and spawning (Olsen *et al.* 2008), is expected to promote fisheries sustainability (Hilborn *et al.* 2003). In summary, population structuring in cod occurs at several hierarchical scales and has been shown to coincide with specific biological adaptations, advocating the need for a Darwinian perspective in fisheries management (Conover and Munch 2002) aimed at conserving such diversity. Thus, technical developments (marker system; sampling design) and the inclusion of markers under selection, and direct analysis of adaptive variation have revealed biologically significant genetic structuring in populations of relatively young evolutionary age (Bigg *et al.* 2008; Pampoulie *et al.* 2008a), and in a species of high dispersal potential. The important point is that even if genetic structuring at neutral loci may be undetected or only weak, biologically meaningful adaptive variation, even on local scales, may still exist (Hutchings *et al.* 2007).

The speed of such adaptive divergence was demonstrated by differential growth (Imsland *et al.* 2004; Case *et al.* 2006; Jorstad *et al.* 2006; Jonsdottir *et al.* 2008) and mortality (Mork and Sundnes 1985a) among different molecular marker genotypes, suggesting rapid adaptive divergence potentially within single cohorts. Similarly rapid adaptation was suggested by temporal differences between year classes in haemoglobin (Mork and Sundnes 1985b) and *Pan I* (Karlsson and Mork 2003) genotypes. Because of such potential for rapid adaptation and commonly observed reductions in age and size at maturity (Trippel 1995), Atlantic cod

also became one of the case studies for demonstrating fishery-induced evolution from probabilistic maturation reaction norms (Olsen *et al.* 2004, 2005), although the inferences of genetic changes have been questioned extensively (Kuparinen and Merilä 2007; Law 2007; Browman *et al.* 2008).

Molecular genetic data of Atlantic cod also clearly show the effects of reduced effective population size, low N_e/N ratio and potentially the local extirpation of a small population. Populations in the Canadian Arctic show lower genetic diversity, but higher differentiation from each other and to cod along the Canadian Atlantic coast (Hardie *et al.* 2006). Similar, but less extreme, patterns can be found in cod inhabiting Gilbert Bay, an isolated embankment in the north of Canada (Beacham *et al.* 2002a). Other populations are weakly differentiated and show a general isolation by distance pattern (Pogson *et al.* 2001; Beacham *et al.* 2002a), suggesting low N_e/N ratios and limited dispersal. Baltic cod, living in a marginal habitat, also show lower genetic diversity than cod from the Atlantic at allozymes, mtDNA and microsatellites, suggesting low N_e and isolation from the Atlantic (Johannesson and Andre 2006). Estimates of N_e/N ratios are low in both the long term (Pampoulie *et al.* 2008a) and the short term (Hutchinson *et al.* 2003), although the latter has been questioned (Poulsen *et al.* 2006). Unusually for a marine species, however, there is evidence for localized overexploitation and possibly extirpation with subsequent recolonization, despite historically large population sizes (Hutchinson *et al.* 2003).

Atlantic cod is clearly a very specialized case study because of the disproportionate research effort that has been invested in this species. The question thus arises whether similar results could be expected in other species if sufficient research is carried out. Atlantic cod show some features that may contribute to genetic patterns of neutral and adaptive genetic differentiation and small effective population sizes: for example, there is tagging evidence for homing behaviour (Windle and Rose 2005) and return migrations between spawning and feeding grounds in many stocks (Robichaud and Rose 2004). Such homing behaviour has also been reported for other fish species (Thorrold *et al.* 2001), although in other species, such as Pacific and Atlantic herring, homing accuracy may be lower (Hay *et al.* 2001), corresponding to weaker population genetic structure restricted to broader geographic scales (Beacham *et al.* 2002b; Ruzzante

et al. 2006). Atlantic cod also show mating behaviour (Rakitin *et al.* 2001; Bekkevold *et al.* 2002; Rowe *et al.* 2008) that may increase the variance in reproductive success and thus reduce the N_e/N ratio (Rowe *et al.* 2007). Unfortunately such detailed biological and behavioural information is not available for most marine fish species. Clearly, there are species for which little population genetic structure (Beacham *et al.* 2002b; Reid *et al.* 2005) and no evidence for low effective population size (Flowers *et al.* 2002) were found despite considerable effort in genetic analyses – such species may therefore show different characteristics in biology or their environment. Nevertheless, the point here is that information on homing, migration, larval dispersal and reproductive success are difficult and expensive to obtain with traditional ecological methods. Genetic approaches provide a fast, easy and relatively cheap first test whether such mechanisms do indeed exist. Atlantic cod is an excellent example for the power of genetic approaches, but care should be taken in drawing conclusions about likely patterns in other species from such data.

Concluding remarks

Technical and analytical advances, combined with an enhanced awareness that neutral markers may underestimate adaptive variation likely to influence recruitment and dynamics, have stimulated important shifts on our view of the biology and evolution of marine fishes. Although high dispersal capacity in many species may influence the potential for local adaptation, gene flow may often be much more restricted than hitherto thought. Moreover, the marine environment, rather than representing open systems that constrain exposure to sustained or marked environmental differences, is more likely to offer a mosaic of divergent and dynamic conditions that can drive marked genetic change, sometimes adaptive, across surprisingly small spatial and temporal scales. Importantly, detection of such genetic and phenotypic diversity is now more feasible and can be examined in relation to identifiable selective forces. Even where this is not directly possible, approaches based on covariance between environmental factors and patterns of genetic structuring (Faubet and Gaggiotti 2008; Selkoe *et al.* 2008) can generate hypotheses for subsequent ecological testing. Such features of genetic flux and adaptive diversity, taken together with the increasing evidence that some marine

fishes may occur in aggregations of remarkably small effective size, underscore the importance of incorporating genetic methodologies and principles more fully into fisheries management.

The undisputed utility of molecular markers in genetic stock identification of many salmonids (Ryman and Utter 1987) has received much less wide-scale application in marine fishes, mainly because generally weak population differentiation in the marine realm (Carvalho and Pitcher 1994). Nevertheless, the notion that genetic and evolutionary processes are only important on a time-scale irrelevant to fisheries management is no longer tenable: major phenotypic shifts and genetic change may occur in decades. It is thus pertinent to distinguish between two major approaches: first, to use molecular markers for the identification of individuals, populations or species and the estimation of demographic parameters, such as gene flow and effective population size; second, to assess functional genetic variability underlying adaptation and the responses to natural and man-made changes in the environment. While both approaches are ultimately united in a focus on the conservation of genetic resources, the former is based primarily on the use of biological tags to estimate diversity and dynamics, whereas the latter is underpinned by the fact that changes in gene frequencies and population dynamics are interdependent (Birch 1960). In consequence, it is important to explore linkages between genetic diversity and processes that govern distribution and abundance: mortality, migration and recruitment. What is perhaps a priority now is to develop an appropriate conceptual framework and analytical tools, especially for meaningful ecological modelling, that can integrate diverse data sets, such as models of biophysical coupling of population connectivity (Galindo *et al.* 2006; Faubet and Gaggiotti 2008; Werner *et al.* 2008) and models of population demography (Andrews *et al.* 2006) to yield management tools of a quantitative and robust nature.

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