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Genetic differentiation, effective population size and gene flow in marine fishes: implications for stock management

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Abstract

Many commercially exploited marine fish and mollusc species exhibit no or a low degree of genetic differentiation in neutral marker genes. This lack of genetic differentiation, typically attributed to high degree of gene flow in marine environments, has sometimes supported the thinking that genetically indistinguishable stocks can be managed as being one panmictic population. Recent comparative studies of neutral marker gene and quantitative trait differentiation in a wide variety of taxa - including several marine organisms - show that a high degree of genetic differentiation (as measured by Q_{ST}) in ecologically and economically important traits is a common place occurrence, even when the degree of differentiation in neutral marker genes (as measured by F_{ST}) is low or absent. In fact, among the empirical studies made so far, the outcome $Q_{ST} > F_{ST}$ is pervasive. This accords with the increasing evidence that natal homing and self-replenishment of local populations may be more common in marine habitats than previously anticipated. If so, the low degree of genetic differentiation in neutral genetic markers could be a simple consequence of the large effective population size (N_e) of many marine populations, effectively buffering them against differentiation due to genetic drift. However, genetic markers linked to parts of the genome under directional selection should readily diverge in allele frequencies especially when N_e is high. In fact, several recent studies have discovered that such loci provide a way to differentiate among stocks undifferentiated in neutral marker genes. Hence, the study of adaptive rather than neutral genetic differentiation among fish and shellfish populations might provide practical tools for stock identification and thereby contribute to improved fisheries policies.

Introduction

The world's seas and marine ecosystems are in a dire state due to human activities (e.g. Roberts, 2007). The footprint of human impact on the world's oceans is strong and widespread (Halpern *et al.*, 2008), and many marine fish populations are fully or over-exploited to the point that declines and stock collapses have occurred (Pauly *et al.*, 2002; Myers and Worm, 2003; Mullon *et al.*, 2005). According to some predictions, all current fisheries will be collapsed by the year 2048 if the exploitation continues at current rates (Worm *et al.*, 2006).

The drastic population size reductions of many fishes due to exploitation will inevitably reduce their effective population sizes (N_e), and hence, increase the risk of loss of genetic variability as observed already in some (e.g. Hauser *et al.*, 2002; Hoarau *et al.*, 2005), but not in all (Poulsen *et al.*, 2006) studied species. Loss of genetic diversity and locally adapted populations (and species) can compromise stability and recovery potential of marine ecosystems, as well as impair their ability to adapt to changing environmental conditions and thereby to their capacity to provide food for the growing human population (Worm *et al.*, 2006). Likewise, by imposing selection towards earlier maturation at smaller size, fisheries are expected to lead to genetic changes and erosion of genetic variation in exploited populations (e.g. Law, 2000; Stokes and Law, 2000; Heino and Godø, 2002; Kuparinen and Merilä, 2007). Such evolutionary changes, if occurring, could also reduce the capacity of populations to recover from over-exploitation (Walsh *et al.*, 2006; Hutchings *et al.*, 2007).

In order to maintain viable and locally adapted fish stocks, proper management policies are needed. To this end, population genetic studies of marine fish populations have assumed an important role in

decision-making (e.g. Waples, 1998; Kenchington *et al.*, 2003; Knutsen *et al.*, 2003; see also: Seeb *et al.*, 2007). Neutral genetic markers can provide valuable information about geographic structuring, gene flow and demographic history of populations, information that can be highly relevant for conservation and management purposes (e.g. Frankham *et al.*, 2002; Kenchington *et al.*, 2003; Maes and Volckaert, 2007). However, the information conveyed by neutral genetic markers is often, or even typically, limited in two important respects. First, if truly neutral, (i.e. unlinked to traits under selection; see below), variability in neutral genetic markers may not provide any information about genetic variability and degree of genetic differentiation in ecologically and economically important traits (Pearman, 2001; Merilä and Crnokrak, 2001; McKay and Latta, 2002; Leinonen *et al.*, 2008). Second, a low degree of genetic differentiation in neutral genetic markers among many populations of marine fishes is a rule rather than an exception (reviews in: Ward *et al.*, 1994; Ward, 2004; see e.g. O'Reilly *et al.*, 2004; Dannewitz *et al.*, 2005; Jørgensen *et al.*, 2005; Florin and Höglund, 2007 for examples of recent case studies), limiting the utility of neutral marker variability in stock identification. In the following, we will focus on these two problems and highlight their implications for practical fish stock management.

1. Neutral marker gene vs. quantitative trait differentiation

Given the logistic difficulties in assessing the genetic basis of ecologically important traits in marine fish populations, estimates of genetic structuring with respect to ecologically important traits are still scarce (Swain and Foote, 1999; Conover *et al.*, 2006). However, there is ample evidence for genetic determination and high degree of genetic variability for fitness-related traits such as size, growth rate and fecundity in marine populations both from aquaculture experiments (Kingham, 1983; Jónasson *et al.*, 1997; Conover, 2000) and from experimental studies of fisheries induced evolution (e.g. Conover and Munch, 2002; Walsh *et al.*, 2006). Further, in those few cases where wild marine fish populations have been tested for local adaptation, even in the absence of any obvious barriers to gene flow, evidence for genetic structuring in respect to quantitative traits has been found (Conover and Present, 1990; Conover 1998; Conover

et al., 2006). Likewise, recent work in freshwater fishes has revealed that even in the face of high levels of gene flow, significant adaptive genetic differentiation can still take place (Saint-Laurent *et al.*, 2003; Hendry and Taylor, 2004).

This evidence set aside, the most general and powerful argument against taking lack of differentiation in neutral genetic markers as evidence for lack of genetic structuring among populations comes from the comparative studies of marker and quantitative genetic differentiation (reviews in: Merilä and Crnokrak, 2001; McKay and Latta, 2002; Leinonen *et al.*, 2008). In the majority of studies covering a wide variety of organisms, the differentiation in genes coding quantitative traits - as measured by the Q_{ST} -index (Spitze, 1993) exceeds that in neutral marker genes (as measured by the F_{ST} -index; Wright, 1951) in many times (Fig. 1A). What is particularly noteworthy in these data is that this difference holds true in the majority of F_{ST} vs. Q_{ST} comparisons where the level of neutral marker gene differentiation is very low ($F_{ST} \leq 0.03$; Fig. 1A) as it typically is for marine fish species (Waples, 1998; Ward, 2004). For this low level of differentiation, Waples (1998) showed that unless very large sample sizes and highly polymorphic markers are available, the paradigm of panmixia is not easily rejected due to lack of statistical power of the tests. Yet, as the data in Fig. 1 shows, substantial genetic differentiation in quantitative traits is possible even when neutral marker genes indicate no differentiation at all.

Although Q_{ST} -estimates from fish studies are still scarce, all available estimates show patterns similar to those from other taxa: Q_{ST} -estimates exceed consistently the F_{ST} -estimates (Fig. 1B). It is noteworthy that all these studies have been conducted in freshwater species, some of which occur also in marine habitats. Given that the F_{ST} -estimates are typically much higher for freshwater than marine species (Ward *et al.*, 1994; DeWoody and Avise, 2000) - and for freshwater populations of species that occur both in marine and freshwater habitats (e.g. Mäkinen *et al.*, 2006) - these observations hint about the possibility that the contrast between the magnitude of genetic differentiation in respect to adaptive and neutral traits in marine populations might be much more pronounced than that in freshwater populations. Some evidence for this is provided by Leinonen *et al.* (2006), who observed higher degree of quantitative

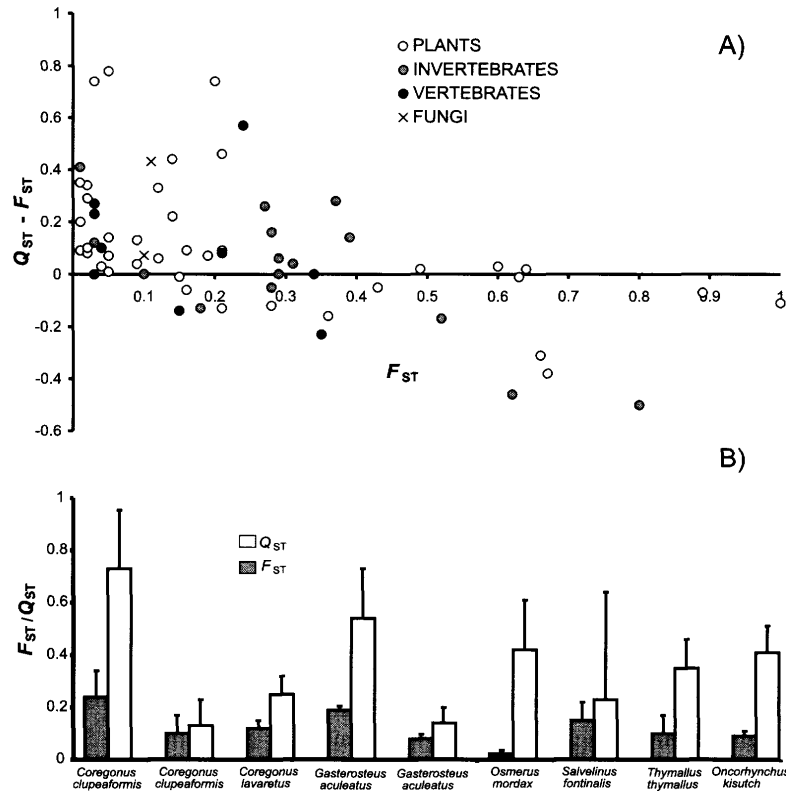


Fig. 1. Comparison of quantitative trait (Q_{ST}) and neutral marker gene (F_{ST}) differentiation in published studies. (a) Difference ($= Q_{ST} - F_{ST}$) divergence estimates as a function of divergence in neutral marker genes (F_{ST}) in different studies (data from Leinonen *et al.*, 2008). (b) F_{ST} and Q_{ST} estimates from published fish studies (data from: Rogers *et al.*, 2002; Koskinen *et al.*, 2002; Østbye *et al.*, 2004; Saint-Laurent *et al.*, 2004; Perry *et al.*, 2005; Leinonen *et al.*, 2006; Raeymaekers *et al.*, 2007; McClelland and Naish, 2007).

trait differentiation among marine than among freshwater populations of three-spined sticklebacks. Also, Luttikhuizen *et al.* (2003) observed a high degree of population differentiation in adaptive traits ($Q_{ST} = 0.4$) in a marine bivalve *Mytilus edulis* with high dispersal capacity and low degree of population structuring in neutral genetic markers ($F_{ST} = 0.02$). Hence, management decisions based solely on the lack of neutral genetic marker differentiation among marine fish (and shellfish) populations would probably lead to poor fisheries policies.

Before turning to proximate explanations for the low degree of neutral marker gene differentiation, we wish to provide a couple of words of warning about the limitations of Q_{ST} -estimates. First, as it can be seen from Fig. 1A, the difference between F_{ST} and Q_{ST} tends to get smaller with increasing F_{ST} . This is expected as the Q_{ST} is bounded to take values in between 0 and 1, and once F_{ST} approaches unity, the difference between the two is reduced unless $Q_{ST} \ll F_{ST}$ (Hendry, 2002). Therefore, in the context of stock identification and detection of locally adapted populations, the best value for efforts invested on estimating

Q_{ST} are gained from systems where F_{ST} s are known to a priori be low. Second, the estimation of Q_{ST} and its standard errors is computationally demanding, and the precision of the estimates is low unless relatively large number of populations are compared (O'Hara and Merilä, 2005; Johansson *et al.*, 2007). Apart from the logistic difficulties with quantitative genetic experiments needed to estimate Q_{ST} , both of the issues mentioned above might limit utility of Q_{ST} in the practical stock identification context. For recent meta-analyses and further discussion on the challenges in Q_{ST} -estimation, see Merilä and Cronkrak (2001) and Leinonen *et al.* (2008).

2. Gene flow or large N_e ?

While low degree of genetic differentiation in neutral genetic markers among many populations of marine fishes is undisputable (e.g. Ward *et al.*, 1994; McQuinn, 1997; Ward and Elliot, 2001; Wirth and Bernatchez, 2001; Knutsen *et al.*, 2003; Nielsen *et al.*, 2003; O'Reilly *et al.*, 2004; Ward, 2004; Dannewitz *et al.*, 2005; Jørgensen *et al.*, 2005; Florin and Höglund, 2007), the causes for this shallow genetic

structuring are not. The low degree of differentiation can result from many factors: high levels of gene flow, large effective population size and/or shared ancestral polymorphism attributable to recent divergence of the populations. While the third explanation may be especially relevant in recently glaciated areas, where the populations are likely to be young (Pogson *et al.*, 2001), it could also apply to more recent population turnover events (Florin and Höglund, 2007). Yet, the lack of significant population differentiation in neutral genetic markers has been traditionally ascribed to high levels of gene flow among marine populations (e.g. Ryman *et al.*, 1984; Ward *et al.*, 1994; Waples, 1998; Ward, 2004). The lack of obvious dispersal barriers in marine environments together with often highly vagile and dispersive larval stages of marine organisms have lead to an impression of high connectivity of marine populations (Palumbi, 1992, 2003). However, this view has been changing recently (e.g. Cowen *et al.*, 2000; Levin, 2006; Metcalfe, 2006; Rocha *et al.*, 2007) and evidence for natal homing (Thorrold *et al.*, 2001; Kraus and Musick, 2001) and self-replenishment has been accumulating (Jones *et al.*, 1999; Swearer *et al.*, 1999; Cowen *et al.*, 2006; Ruzzante *et al.*, 2006). Hence, high gene flow as a general explanation for the shallow genetic structuring of marine populations is becoming tenuous.

A low degree of genetic differentiation among populations of marine species could also be attributed

to large effective population sizes, which would be expected to limit differentiation due to genetic drift (e.g. Allendorf and Phelps, 1981; DeWoody and Avise, 2000). In fact, both high levels of gene flow, and large N_e s in absence of gene flow are expected to leave similar signature on the genetic structure of populations. This is illustrated by the simulation results presented in Fig. 2: with N_e s of several thousands, the F_{ST} will remain low even in absence of migration (Fig. 2). Hence, a low degree of genetic differentiation is expected also in the absence of gene flow if N_e is large. The reason for this is that large N_e makes genetic drift an inefficient force in altering allele frequencies over space and time, and it will take roughly N_e generations before reaching drift-migration equilibrium (e.g. Crow, 1986). Hence, allele frequencies in neutral loci in large populations are slow to change. Yet – as pointed out above - even in cases where F_{ST} is close to zero and $mN_e > 20$, divergent (e.g. dotted line in Fig. 2) selection can lead to adaptive population differentiation as has been shown for the three-spined stickleback (*Gasterosteus aculeatus*; Hendry and Taylor, 2004) and rainbow smelt (*Osmerus mordax*) populations (Saint-Laurent *et al.*, 2003).

3. N_e of marine fish populations

What do we know about the effective size of marine populations? For many commercially important species, such as Atlantic cod, the possibility of hav-

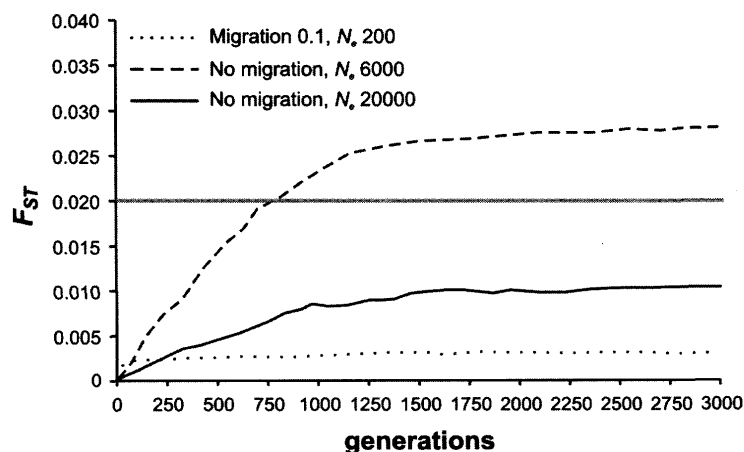


Fig. 2. A simulated example illustrating the expected influence of gene flow and effective population size on neutral marker gene differentiation (F_{ST}). Changes in F_{ST} between two populations over 3000 generations are shown, assuming different amounts of gene flow and different effective size (N_e) of populations. Each line represents an average of 100 simulations based on seven highly-polymorphic loci. Calculations assume an equal sex ratio, no mutation, random mating, free recombination and 15 possible allelic states. The grey line represents the median F_{ST} value for marine fish populations (Ward, 2004). Simulations were carried out with program EASYPOP (Balloux, 2002).

ing small N_e s is quite unlikely, considering their large census population sizes and the strong fishing pressure that they have supported for centuries (Richardson and Gold, 1993; Pogson *et al.*, 2001; but see Hutchinson *et al.*, 2003). In fact, a recent study suggests that the effective size of local cod populations is likely to exceed several thousands of individuals (Poulsen *et al.*, 2006). Estimates for other marine species are still scarce (Hauser *et al.*, 2002; Turner *et al.*, 2002; Árnason, 2004; Hoarau *et al.*, 2005), and sometimes turned out to be surprisingly small (e.g. Turner *et al.*, 2002). However, given the methodological difficulties involved in estimation of N_e with the temporal method (e.g. sampling strategy & technical artefacts, migration and cryptic population structure; see Poulsen *et al.*, 2006 for detailed discussion), some caution should be exercised in attaching too much weight on individual estimates. Although we are still far from having a satisfactory picture about N_e s in marine fish, the logical possibility of large N_e s constraining neutral population differentiation should not be overlooked and more research would be needed on this issue.

4. Future Research needs

In our view, the main challenge for the future studies of population structuring in marine organisms is in estimating the degree of population differentiation in genes coding quantitative traits. Two basic approaches are obvious:

First, common-garden (aquaculture) experiments with fish from different origins allow estimation of the degree of additive genetic variability within and among populations and thereby Q_{ST} . Albeit a logistical challenge, this approach should be feasible even for many marine fishes (see: Conover *et al.*, 2006 and their Table 1 for compilation of such experiments in marine fishes) and for molluscs in particular, because numerous species are routinely reared in aquacultures (e.g. Guo *et al.*, 1999). Even in the absence of estimates of within and among population estimates of additive genetic variability for quantitative traits, some useful inference about the magnitude of Q_{ST} may still be possible if reasonable assumptions about genetic *vs.* environmental influences on phenotypic trait means can be made (e.g. Merilä, 1997; Bernatchez, 2003; Cano *et al.*, 2008; Leinonen *et al.*, 2008). Yet, care should be taken with the inferences as environmental effects on fish phenotypes are pervasive

(e.g. Swain and Foote, 1999), and often geographically structured too (Conover, 1998; Conover *et al.*, 2006).

Second, genomic approaches - such as genome scans (Schlötterer, 2003) or gene expression studies (e.g. Whitehead and Crawford, 2006; Hoffmann and Daborn, 2007) - which have recently become an area of important research (e.g. Beaumont and Balding, 2004; Larsen *et al.*, 2008) provide another path for gaining information about adaptive divergence among stocks showing little differentiation in neutral genetic markers. The idea behind genome scans is that putative neutral genetic markers, such as microsatellites, will exhibit less allelic variation and more population differentiation than under neutral expectation if they are linked to selected sites (i.e. genes coding for traits of adaptive value). This phenomenon is known as hitchhiking or selective sweep (Schlötterer, 2003; Beaumont and Balding, 2004). Genome scan approaches could be expected to be of particular utility in finding signatures of selective events - and thereby also useful markers for stock-identification - in marine species because of their large effective population sizes. This is because even weak selection can overrule the effect of genetic drift in large populations (Endler, 1986) and, thereby, increase the chance of the detection of selective sweeps. Genome scan studies are still rare in marine fishes (but see: Mäkinen *et al.*, 2008a,b), but hitch-hiking selection on two loci has been documented in the Atlantic cod (Nielsen *et al.*, 2006; Westgaard and Fevolden, 2007). On the basis of these loci, Westgaard and Fevolden (2007) inferred that Norwegian coastal and North East Arctic cods at Barents Sea form two distinct management units.

Genome scan studies can be complemented with candidate gene approaches (Coussens and Nobis, 2002) by sequencing the genomic regions next to detected selective sweeps and matching them against gene sequences identified from other species and/or available in databases such as GenBank (see: Mäkinen *et al.*, 2008b for an example). In this way, it is possible to identify genomic regions containing genes coding for phenotypic traits (i.e. functional candidates) and use these in stock differentiation. From a stock management perspective, genome scan approaches should be prioritised at local scales, rather than involving populations across large geographical distances, since is at the microgeographical level

where neutral markers usually fail to detect significant population structure (Lundy *et al.*, 1999; Knutsen *et al.*, 2003; Nielsen *et al.*, 2004).

Finally, more information about effective population sizes and actual migration rates are obviously needed to test the hypothesis about the buffering effect of large N_e on population differentiation in marine fishes. Studies such as those by Hauser *et al.* (2002), Turner *et al.* (2002), Árnason (2004) and Nielsen *et al.* (2006) based on the observed changes of marker allele frequencies over time (i.e. temporal approach, Krimbas and Tsakas, 1971) show the way. However, as temporal methods estimate N_e according to the rate of allele frequencies change, migration can cause a population to behave as if strong drift was changing allele frequencies, resulting in underestimation of N_e (Wang and Whitlock, 2003). Fortunately, recent methodological and theoretical developments allow N_e s and migration rates to be estimated separately if reasonably large sample sizes and many markers are available (Wang and Whitlock, 2003). Nevertheless, if marine fish populations indeed have large N_e s, changes in allele frequencies may be hard to estimate. Yet, the temporal approach still can provide useful insight about relative sizes of exploited and less exploited populations, as well as of the relative roles of migration and N_e in modulating divergence or lack thereof.

5. Conclusions

In conclusion, it is conceivable that fisheries management decisions based on the assessment of neutral genetic variability alone can lead to the loss of genetic biodiversity (i.e. locally adapted populations/stocks) due to the fact that neutral markers can fail to recognize locally adapted populations/stocks. Hence, sustainable fisheries management should invest more effort in evaluating the genetic basis for quantitative trait differentiation (e.g. age and size at maturity), and not rely solely on inference drawn from neutral genetic markers. This is in line with the *precautionary principle*, according to which the lack of scientific information on potentially adverse effects on genetic diversity should not be used as a reason to prevent or postpone measures to avoid or minimize such negative effects (FAO, 1996; Convention on Biological Diversity, 1992; Cartagena protocol on biosafety, 2000; Powles *et al.*, 2000). In other words, clear phenotypic differences among fish - and perhaps even

among marine mollusc - stocks should be considered as indicative of genetic differentiation until otherwise proven. This is also consistent with the principles of effective fisheries management in which distinct stocks are managed separately to optimize their yield.

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