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NEWS AND COMMENTARY

Adaptive peaks in a flat-fish

Adaptive divergence overcoming gene flow

L Zane

By contrasting the pattern of genetic structure at putatively neutral microsatellites with the pattern at the heat-shock cognate protein (*Hsc70*), Hemmer-Hansen and colleagues on page 592 of this issue of *Heredity*, convincingly show the existence of adaptive divergence despite high gene flow in the European flounder *Platichthys flesus*. This result is unexpected because if gene flow is high it should preclude local adaptations by rapidly blurring allelic frequency differences between populations. If gene flow is the dominant force controlling both, the pattern of genetic structure inferred with neutral markers is thus expected to coincide with the pattern at loci under selection (Conover *et al.*, 2006). This relationship provides the basis for using information from population genetic studies with neutral markers in the context of conservation of marine resources and fisheries management. The Hemmer-Hansen study now clearly shows not only that local adaptation is possible in the sea, but also that patterns of differentiation at selected and neutral markers can be strikingly different. This means that current management practice could misidentify management units, leading to erosion of genetic resources.

This study comes at a time of exciting research on the population genetics of marine organisms. With the increased application of molecular tools, many commonly accepted perceptions have been challenged in the field. Starting from the general belief that populations of marine organisms, being large and inhabiting an environment with no obvious barriers to genetic flow, are essentially homogeneous with at most a pattern of isolation by distance shaped by the duration of larval dispersal, we are now facing a much more complex picture. The wide application of microsatellites allows us to easily measure the connectivity between marine populations, resulting in the detection of significant albeit weak genetic differentiation. It also allows us to estimate the

importance of larval retention in local areas, questioning the idea that dispersal is determined by the extent of larval duration only. In addition, the finding of a very small effective population size in many abundant species and the existence of trends of loss of genetic variation over time, disputes the idea that these species are characterized by large population sizes and thus are not prone to genetic erosion. Finally, the occurrence of rapid contemporary evolution mediated both by environmental and human-related selective pressures, and the emerging body of evidence that indicates the importance of behaviour at the larval and adult stage in shaping the structure of marine populations, identifies a complicated situation.

In this context, using a candidate gene approach, Hemmer-Hansen *et al.* (2007) compared the pattern of genetic variation at eleven microsatellites with that at one intron of *Hsc70*, a gene involved in the response to thermal/osmotic stress and pollution.

Analysing population samples from the north-eastern Atlantic, the authors found a fivefold higher genetic differentiation, measured by F_{ST}, at *Hsc70* than at the microsatellites. When the confidence interval of single locus divergence was reconstructed under the neutrality hypothesis, *Hsc70* was identified as a strong outlier, indicating the existence of directional selection. Notably, the result of higher differentiation at *Hsc70* is even stronger after the standardization of genetic divergence, taking into account the maximum divergence attainable at each locus. With this approach, the authors corrected a possible bias resulting from microsatellites' hypervariability, because maximum divergence is limited by the observed homozygosity of the subpopulations (Hedrick, 2005). In this respect, this study augments similar results recently obtained for another putatively selected locus, the pantophysin locus (*PanI*), in the walleye pollock

(Canino *et al.*, 2005), by showing that the observed higher divergence at functional genes is not due to a comparison between markers with different mutational properties.

Importantly, Hemmer-Hansen *et al.* (2007) also found strong differences in the pattern of genetic structure between neutral and selected loci. Thus, the results of this study differ from that obtained with the *PanI* locus in cod around Iceland (Pampoulie *et al.*, 2006), where a standardized higher differentiation was found at *PanI* with respect to microsatellites, but the pattern of differentiation was congruent between the two sets of loci. In that case, the authors concluded that oceanographic and environmental factors acted together in shaping genetic diversity in that species. In the European flounder instead, comparisons of samples from the western and central Baltic with those of the North Atlantic detected strong differences: neutral markers suggest homogeneity between the three locations, while *Hsc70* reveal a sharp break in allelic frequencies. This pattern is striking because of the temperature/salinity gradient occurring in the Baltic Sea, which could represent the selective force acting on *Hsc70*.

The exact evolutionary and conservation implications of the Hemmer-Hansen results are still unresolved and depend on the understanding if selection pressures occurred in the past and the populations have not yet attained equilibrium, or if selection is currently taking place. This question could be answered by comparing the performance of different genotypes in different salinity/temperature conditions in common garden experiments that, of course, can be difficult with an organism like flounder. At present, Hemmer-Hansen *et al.* (2007) argue that migration-drift equilibrium has been reached at neutral markers in the investigated samples, citing both the observed strong differences in microsatellites among several samples and comparisons with other species in the same environmental setting. As allelic frequencies tend to approach equilibrium much faster in loci under selection than in neutral loci, the message is that the higher differentiation at *Hsc70* is maintained by contemporary selection. In this case, it is important to recall that, at equilibrium, F_{ST} is inversely related to Nm, the product of effective population size N for the proportion m of immigrants. Therefore, estimates of effective population size and application of realistic

models of gene flow are needed to estimate m and quantify the genetic cost of immigration for the populations and its possibility to preclude local optimal adaptation. In this regard, it is noticeable that the Baltic populations, on which the apparent selection takes place, are not fixed for a specific allele of *Hsc70*. Then, if populations are at equilibrium, a cost in terms of mortality linked to gene flow may be present, and, considering that at the genome wide level many loci can be under selection, the genetic load experienced by the population might be extremely high. Thus, if the existence of local adaptation is generally confirmed, an important link between population genetics and dynamics can be foreseen, and the application of both selected and neutral markers will be needed to effectively resolve the stock structure of marine fish.

Dr L Zane is at the Department of Biology, University of Padova, Via G. Colombo 3, Padova I-35121, Italy.

e-mail: lorenz@civ.bio.unipd.it

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Editor's suggested reading

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