

**Genetic Structure among Eastern Oyster Populations
and the Genetic Health of Chesapeake Oysters**

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Testimony
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Species

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I have been asked to summarize my research on the eastern oyster, *Crassostrea virginica*, as it pertains to the health of Chesapeake Bay populations, evidence for population structure, and the scientific basis for designating subspecies. I am a geneticist who uses genes to understand organisms and population histories, rather than focusing on the intricate workings of the genes themselves; Thus, I will speak of genetic markers, and by this I mean segments of DNA that trace their ancestry through the extended pedigree of a population and can therefore be used as markers of migration and genetic drift.

I have been working on eastern oysters since 1991. Most of what I will report today has been published in the peer-reviewed literature by myself and others. However, I will also report on NOAA/Sea Grant -funded research on Chesapeake Bay oysters that is currently under peer review as well as preliminary results that bear directly on the questions at hand. My use of the term oyster will always refer to *C. virginica* unless otherwise indicated.

My testimony will be in three parts. I will begin with a very brief summary of those biological attributes of oysters that most directly affect their propensity for dispersal, population admixture and population viability. Second, I will summarize the evidence for distinct oyster populations in the Atlantic and Gulf of Mexico. Third, I will provide my evaluation of the genetic health of Chesapeake Bay oyster populations.

Eastern oysters are a very old species, proliferating in estuarine waters for the last 20 million years while many other mollusk species have come and gone in the western Atlantic. It is remarkable that such a successful species can now be imperiled by the cumulative effects of human activities, so it is instructive to examine the characteristics of oysters that have probably conferred evolutionary success. Eastern oysters are extremely fecund, with females routinely producing 25 million eggs each year. This not only provides a capacity for prolific population growth under good conditions, but the genetic diversity generated among those eggs by meiotic recombination also buffers oysters against environmental heterogeneity. Oysters begin life as a larva that feeds in the water column for two to three weeks before locating suitable hard substrate and cementing itself for the rest of its sessile existence. Depending on tidal and ocean currents, a three week duration in the water column could disperse the average oyster larva hundreds of kilometers, promoting population connectivity. Although there is good evidence that larvae do not drift as passive particles, but rather swim vertically to effect retention within tidal estuaries, only recently have we had the proper genetic markers and analytical power to measure these effects in wild populations. Finally, the oyster has a very plastic phenotype. In the same way that it grows its shell in whatever configuration the substrate and adjacent organisms allow, its physiology and growth is also modified in response to the local salinity, temperature, etc. The eastern oyster has physiological limits, for example it does not survive well at oceanic salinities, but the broad geographic range of this species from New Brunswick, Canada to Yucutan, Mexico, speaks to its evolutionary success as a generalist.

The population genetics of oysters has been studied more extensively than nearly any other native marine invertebrate in US waters. This interest did not stem primarily

from the commercial value of this species, but rather because of the population biology described above, and was further instigated by scientific controversies over interpretation of the observed population genetic patterns (Appendix 1). In total, genetic markers have shown every imaginable pattern of variation when compared across Atlantic and Gulf of Mexico (Gulf hereafter) populations—from homogeneity across the regions to alternate fixation for different DNA sequences. This latter pattern means that for a particular gene (for 26 genes, in fact, all on the maternally-inherited mitochondrial DNA) the Atlantic and Gulf populations do not share any of the same DNA sequences. It is conventional to interpret this genetic exclusivity under the assumption that it was produced by genetic drift over an extended period of reproductive isolation. Doing so in this case leads to an estimate that Atlantic and Gulf populations became isolated approximately 1.2 million years ago and evolved independently in isolation until relatively recently. Many other genes show strong differentiation between Atlantic and Gulf oysters – our preliminary estimate is that two to four percent of genes in the oyster genome show extreme differentiation despite the fact that these populations are now reunited and exchanging some migrants.

In eastern Florida, where the historically Atlantic and Gulf populations now converge, genetic variation shows a sharp geographic transition (50 to 75 percent gene frequency shift over 20 km; Figure 1). In a species such as the oyster with the capacity for long distance dispersal via larval drift, this sharp and stable genetic transition is only possible if physical conditions along eastern Florida truncate dispersal distances (i.e., a dispersal barrier) and/or strong natural selection maintains the genetic distinctions that have evolved between Atlantic and Gulf oysters. Research in my laboratory is currently focused on measuring the relative importance of these two factors. I suspect that both are important, but one recent result will illustrate how selection may be differentially favoring different oyster phenotypes across this latitudinal transition. We compared growth rate of Atlantic-like and Gulf-like oysters in two locations, one north of the genetic transition and another site south of the transition along eastern Florida. Growth rate is widely considered to be an important phenotypic determinant of overall fitness in bivalve mollusks, with faster growth leading to an advantage in competition for space, larger body size, greater fecundity, and a higher probability of producing successful offspring. After taking into account complicating factors such as the density of oysters, our preliminary results indicated that these two populations of oysters each grew faster as juveniles in their home environment than in the foreign environment. This is the definition of local adaptation; genetically-determined higher performance leading to higher relative fitness in one environment relative to another. These results provide the first experimental indication that oysters in the Atlantic and Gulf of Mexico are locally adapted to their environments, but conclusions must remain tentative until the experiments are replicated with controls for potential confounding factors.

My final comments pertain to the Chesapeake Bay population of eastern oysters, arguably the most anthropogenically degraded and depauperate population in the species. I speak of it as a population out of convenience, not because of any evidence or belief that it is demographically isolated from adjacent stocks along the Atlantic coasts of Virginia and Maryland. The potentially broad larval dispersal of oysters has always led to

the assumption that Chesapeake Bay oysters all evolved as a single interbreeding unit, at least on an evolutionary time frame. Several published genetic studies supported this assumption because evidence for population structure within the Bay was nonexistent or weak. We examined DNA markers with greater sensitivity than had been examined before and found the first evidence that oysters in different parts of the Bay evolve somewhat independently. Specifically, we found that the amount of genetic divergence between two Chesapeake Bay oyster samples depends on their physical proximity. Two samples in adjacent tributaries show greater relatedness than two samples from different sides of the Bay. This result is consistent with theoretical expectations for continuously distributed populations in which migrants are primarily shared among adjacent sites. The implications of this result are quite profound for restoration of oysters because they imply that even on a time scale of decades, the vast bulk of dispersing larvae that successfully settle, grow and reproduce are staying close to home—probably remaining within the same Chesapeake tributary where the parents were. Our results indicate that local dispersal is not only a feature of oysters in a few ‘trap-like’ tributaries, but rather a general characteristic of oyster populations in the Chesapeake. The good news is that restoration efforts directed locally within a tributary or region are likely to have local payoffs, rather than having the effort dissipated when larvae scatter. The bad news is that this type of population structure, coupled with the fact that oyster populations are severely reduced and fragmented today in the Chesapeake, makes the risks of inbreeding and genetic deterioration of the population a serious concern.

Inbreeding in natural oyster populations and its consequences is a complicated subject that is under active investigation in several laboratories. My work on Chesapeake Bay oysters shows that they have retained large amounts of genetic variation compared with populations outside the Bay. Thus, the most obvious indication of inbreeding risks, the loss of genetic diversity, is rejected. However, much more subtle inbreeding effects are predicted by theory in this species and these have not been examined. Also, the increased planting of hatchery-bred stock exacerbates the population fragmentation by introducing genetically depauperate stocks. Furthermore, the recent move by the Army Corps of Engineers and other restoration biologists to plant selectively-bred, disease tolerant strains of *C. virginica* for restoration is likely to further lower the overall genetic health of Chesapeake Bay oysters (with the hope of infusing genes underlying disease tolerance into wild stocks, a highly speculative proposition). Thus, to summarize, I would say that inbreeding is not currently the most serious risk to Chesapeake Bay oysters – environmental degradation and disease take that prize. Nonetheless, there is no such thing as “the end justifies the means” in restoration biology; the degree of long term success we can expect from restoration will depend on the means we take to get there. Unfortunately, there are no simple, quick or inexpensive solutions.

Appendix 1

One controversial hypothesis regarding oysters involved the interpretation of genetic patterns of population structure. I summarize the controversy here in an effort to clarify the issue and suggest its resolution so that it does not unduly muddy the deliberations on population distinctions. In Atlantic and Gulf oysters are genetically homogeneous when examined with some genetic markers, whereas other genes show strong differentiation. It is expected that genes on different chromosomes can evolve independently within the same set of populations and might be shaped by different evolutionary forces (e.g., selection, genetic drift) into various patterns of population structure. So pattern variation among markers is not controversial, but one study found different levels of Atlantic – Gulf differentiation in two classes of markers (protein-level polymorphisms in metabolic enzymes versus polymorphisms in nonfunctional DNA). I think it is fair to say that subsequent work has rejected the hypothesis that certain classes of genetic marker are shaped by distinct evolutionary forces in oysters. Instead, it appears that the evolutionary history of these populations, in which Atlantic and Gulf oysters evolved in isolation for a considerable period and recently reunited, has created widely varying patterns of differentiation among genes.

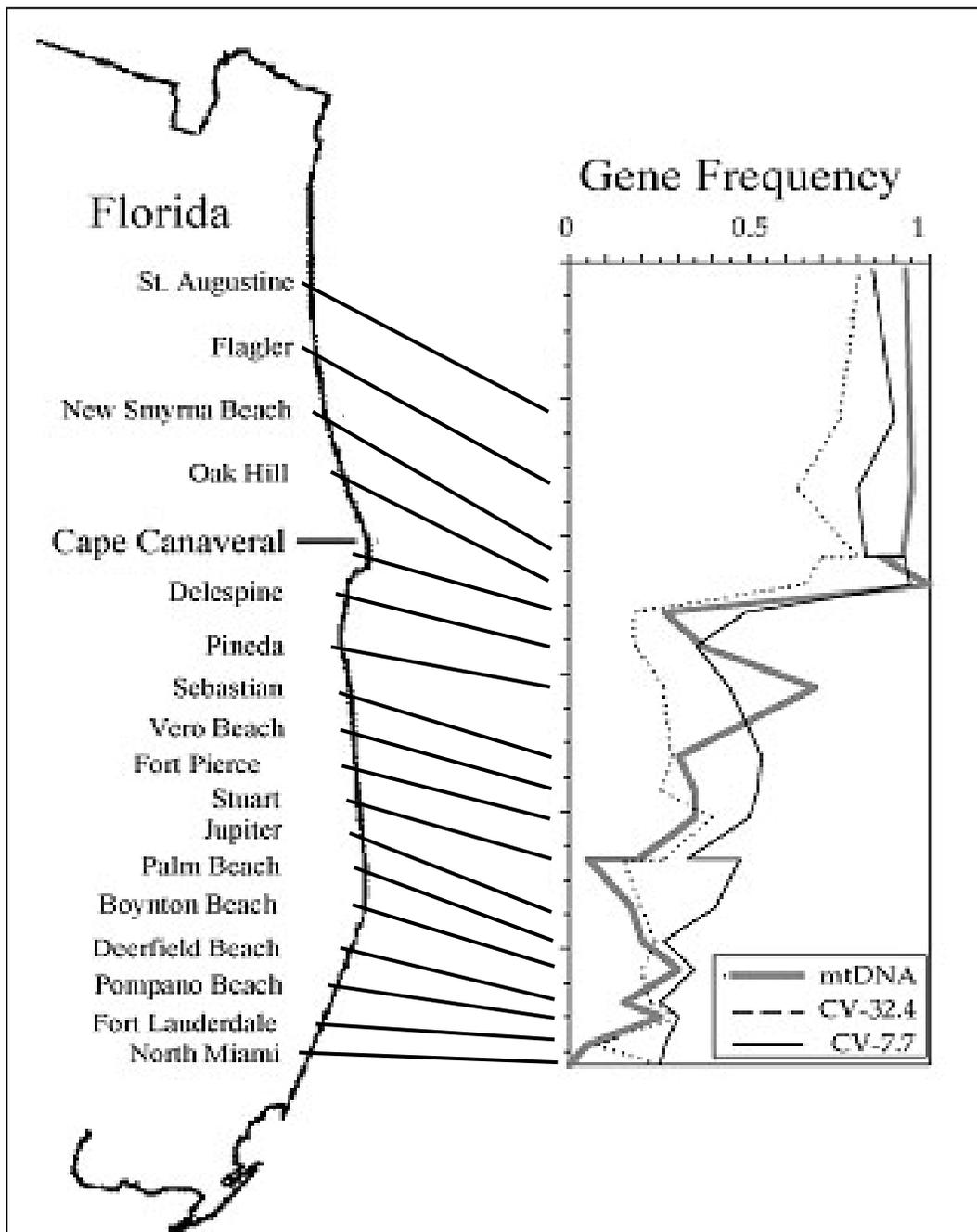


Figure 1. Gene frequency clines for one mitochondrial (mtDNA) and two nuclear loci shown in relation to the eastern Florida geography (samples collected in 1991; Hare and Avise 1996, *Evolution* 50:2305-2315).