

# Genetic markers trace the origin of *Mnemiopsis* spp in Eurasian waters

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Changing environmental conditions, worldwide transport by commercial ships provide the basis for the increasing rates of marine invasions with substantial impact of marine ecosystems. Here we focus on the comb jelly *Mnemiopsis leidyi* one of the most prominent marine invaders worldwide.

Marine invasions continue at an ever increasing rate. The driving forces are the transport of propagules, larvae or adults of non-indigenous marine organisms, predominantly via ballast waters of cargo ships. This unintentional globalization leads to local re-assembly of marine biodiversity, with coastal areas often being the host of more non-indigenous species than native ones. More importantly, the homogenization of marine habitat has the potential to completely restructure food webs and to alter ecosystem functioning. One striking case in point is introductions of the comb jelly *Mnemiopsis leidyi* (Fig. 1) from American coasts of Atlantic to Eurasia, starting in the 1980s. This zooplanktivorous species is able to consume the complete secondary production when it reaches high densities in its native habitat along the US east coast. Hence, when some years after the first observation in Black, Azov and Caspian Sea, the zooplanktivorous fish stocks collapsed, with concomitant severe socio-economic consequences. However, additional anthropogenic influences for the jellyfication of these seas such as overfishing, eutrophication and climate warming cannot be dismissed.

One first key information in invasion biology are the questions (i) from where the inoculum originated (ii) whether the invasion has had single or multiple origins and (iii) whether or not the invader species in its new location is genetically depauperate compared to the native habitat. In particular the two latter questions refer to a role of genetic and evolutionary processes that can determine the success and hence, the impact of an invasive population. For example, there is evidence that upon mixing of several genetically distinct invasion waves (hybridization), 'super'-genotypes with a much stronger ecological performance and environmental tolerance may exacerbate the effects of the newcomers. As a counteracting process, the loss of genetic variation through a genetic bottleneck, as expected in an invasion with a small inoculum size, should decrease the adaptive potential of invaders.

We set out to address above questions in the recent invasion of *Mnemiopsis* spp into North- and Baltic Sea, where the species was first recorded four years ago. Given the history of earlier *Mnemiopsis* invasion, the ecological consequences of this species in its new habitat are of high concern to marine ecol-

ogy and management. As a prerequisite to answer above questions, we first developed high-resolution molecular genetic markers (microsatellites) that are able to measure population affiliation, genetic distinctness



Figure 1: *Mnemiopsis leidyi* from the Baltic Sea, Photo: J. Javidpour.

and genetic diversity in population samples. For the first time in the phylum *Ctenophora* (comb jellies), these microsatellites were applied to samples coming from 13 native and invaded locations collected in 2008 and 2009.

With respect to the origin of invasion, the genetic patterns revealed a very clear-cut picture (Fig. 2). There were clearly two major invasion waves, one earlier with an origin close to the Gulf of Mexico, which then reached the Black and Azov Sea in the 1980s. From there, in a stepping-stone manner, specimens reached the Caspian Sea in the late 1990s. In contrast, the recent invasion to the North- and Baltic Sea had an independent origin. With a completely independent source

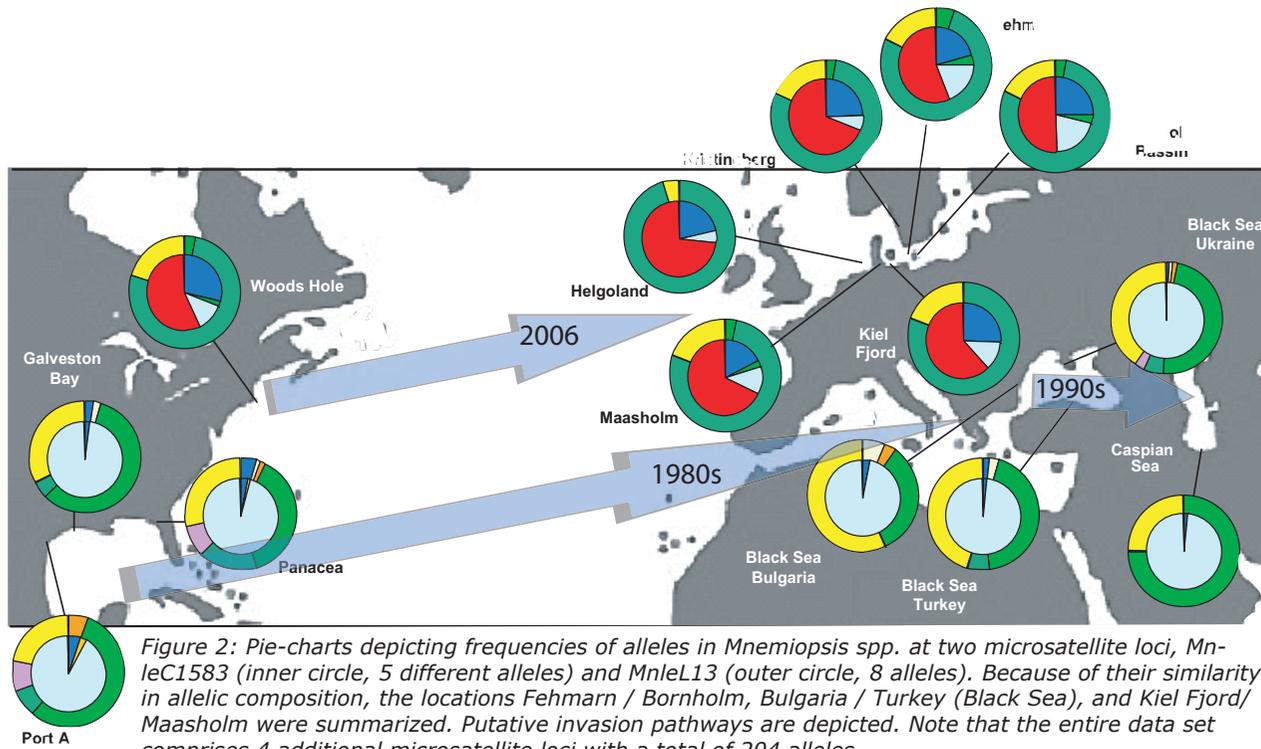


Figure 2: Pie-charts depicting frequencies of alleles in *Mnemiopsis* spp. at two microsatellite loci, *MnleC1583* (inner circle, 5 different alleles) and *MnleL13* (outer circle, 8 alleles). Because of their similarity in allelic composition, the locations Fehmarn / Bornholm, Bulgaria / Turkey (Black Sea), and Kiel Fjord/ Maasholm were summarized. Putative invasion pathways are depicted. Note that the entire data set comprises 4 additional microsatellite loci with a total of 204 alleles.

population, individuals were transported from a location in New England to Northern European shores. In fact, we cannot measure any genetic differentiation between the samples taken in Woods Hole versus the south-western Baltic near Kiel. Interestingly, the North Sea is comprised of a somewhat different and genetically less diverse gene pool which clearly indicates that the Baltic Sea population is not a spill-over of the North Sea. At present, there is no indication that these two invasion waves have mixed. Nevertheless, new reports of *Mnemiopsis* from the western Mediterranean Sea indicate a potential mix-

ing area, a question that we will closely monitor in the near future.

As for the genetic diversity, it is interesting that the earlier invasion revealed a classical reduction in both the number of alleles at the microsatellite markers, and of the heterozygosity. While the source populations in the Gulf of Mexico region reveal on average 9.6 alleles / locus, this drops to 6 alleles in the Caspian Sea population. However, there is no indication that the genetic diversity in the Baltic Sea is reduced compared to New England. These results demonstrate that even within the same taxon, the comb jelly *Mne-*

miopsis, we find a genetic bottleneck in one invasion wave, but not in the other.

Moreover the identification of two rather distinct source gene pools along the US East coast has taxonomic implications. The Gulf coast is inhabited by a morphologically identified different *Mnemiopsis* species, *M. mccradyi* (Meyer 1900), which has recently been questioned based on DNA barcoding sequences. Our microsatellite data, in contrast, call for a reconsideration of two different species that occur along the US East coast, a more northern one (*M. leidy*), and a southern one (*M. mccradyi*). Clearly, more taxonomical, ultrastructural and molecular genetic work needs to be done before the taxonomic status of the *Mnemiopsis* taxa can be resolved.

Our future work will address the question of rapid adaptation of invasive populations to their new habitat. Can we already find molecular genetic adaptation in selectively relevant genes between individuals from the native habitat, and after either 20 yrs, or 4 yrs of selection in the Black or Baltic Sea, respectively? These data will shed light on the amazing ecological and evolutionary adaptability of many invasive species that seem to contradict the concept of a tight match between a species niche and its environment.

## Reference

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