Does stress tolerance in invasive marine species differ between populations from the native and the introduced range?

The introduction of species to ranges in which they were not native in historical times by human vectors is occurring worldwide - in both terrestrial and aquatic habitats - and with an increasing frequency (Ruiz et al. 2000, Occhipinti-Ambrogi & Savini 2003). However, only a small number of the introduced species spread and become invasive in their new environment (Williamson & Fitter 1996). The question which traits make a species a successful invader is of great interest for ecologist and the answer to it should help to predict and manage future bio-invasions. It is generally assumed that a broad tolerance towards environmental stress, high reproductive rates, and plasticity increase invasiveness (e.g. Stachowicz & Byrnes 2006). In addition to this, a species may have the capacity to adjust to a new environment during the course of generations, what might explain the time gap between introduction and spread that has been observed for many non-indigenous organisms (Mack et al. 2000, Mooney & Cleland 2001). To identify the traits and processes that lead to the survival, spread, and establishment of species in an ecosystem to which they are not native, it is promising to compare the performance of invaders both in their introduced and native range (Hierro & Maron 2005). However, most studies on alien species were conducted in their invasive range only and knowledge about the ecology of such organisms in their native environment is frequently missing (but see Henkel et al. 2009, Vermeij et al. 2009). Biogeographical comparisons have been done in terrestrial systems, were invasive plant populations were contrasted with native populations with regard to their associated arthropod communities (Cripps & Schwarzländer 2006), associated soil communities (Reinhart et al. 2003), population density and size (Beckmann & Erfmeier 2009), and competitive abilities (Barney et al. 2009). In the marine environment the number of such comparisons is limited: Perez et al. (1988), Hay & Villouta (1993), and Henkel et al. (2009) investigated traits of the brown alga *Undaria pinnitifida* in individuals stemming from the donor region (southeast asia) and its invasive range in Europe, New Zealand, and the North-American west coast, respectively. While Hay & Villouta (1993) compared the timing of zoospore liberation and gametogenesis of New Zealand and Asian populations, Henkel et al. (2009) focussed on the production of heat-shock proteins as a response to thermal stress. Both studies, however, did not reveal differences in the investigated parameters between seaweed individuals from the different ranges.

Tolerance towards abiotic stress, such as fluctuations in temperature and ambient salinity, is viewed as a key trait of marine invasive species, but it remains unresolved whether invasive species generally show a higher tolerance in their introduced or in their home range. Here, two competing models predict two diverging outcomes of this comparison. Invasive populations could be more stress tolerant, since the founder population went through a stressful transfer and maybe only stress tolerant genotypes survived the passage. On the other hand, it could be that invasive populations are less stress tolerant than native ones, since they often have a lower genetic diversity and therefore a reduced capacity for selective adaptation to physical stressors.

In the frame of the coming GAME project, we want to compare the performance of invasive species in the face of abiotic stress in their native and in their introduced range. Depending on the outcome, this should enable us to give either support for one of the two concepts or it will show that stress tolerance in a founder population is not influenced by consequences of the transfer. If the population in its introduced range is more tolerant than in its native range, this can be explained by the selection of stress resistant genoytpes. The inversed scenario, however, would suggest that a reduced genotypic diversity/ genetic impoverishment leads to a decrease in stress tolerance.

For this study, we need to identify which stations in the GAME-network are located in the native or in the invasive range of one or more marine invertebrates or macroalgae. For this, we attached a table to this email, which should be completed by all our partners. The following compilation of species, which could be suitable for our purposes, already indicates the broad taxonomic range we could cover: *Sargassum muticum, Undaria pinnitifida, Gracilaria vermiculophylla, Caulerpa taxifolia, Codium fragile, Mytilus galloprovincialis, Mytilus edulis, Perna perna, Crassostrea gigas, Elminius modestus, Balanus amphitrite, Carcinus maenas, Eriocheir sinensis, Bugula neritina, Watersipora arcuata, Styela clava, Stylea plicata, Ciona intestinalies, Molgula sp., Didemnum sp.*

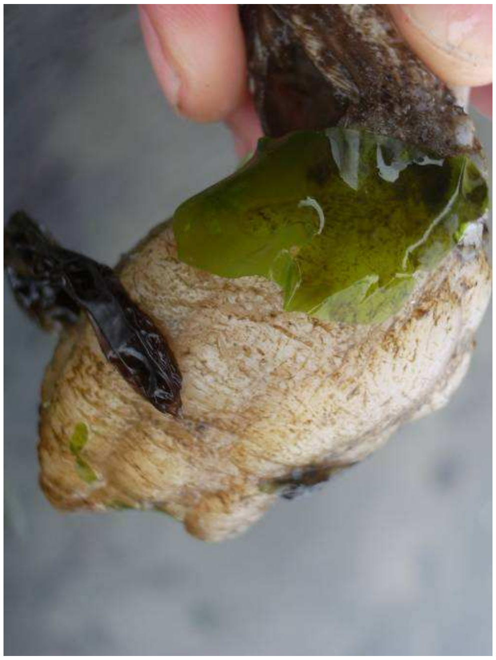

Figure 1: The tunicate *Styela sp*. is a globally abundant invader that can be found in many coastal ecosystems. Photo: Mark Lenz

The material and methods should largely follow the approaches chosen for the previous GAME project. The above-mentioned hypotheses will then be tested in short-term experiments, which can be conducted in indoor aquaria systems, outdoor mesocosm facilities or, in some cases, in the sea. Stressors could be salinity stress (relevant in areas with high and frequent precipitation affecting shallow water or intertidal habitats), low-light stress (common in subtidal habitats prone to fluctuations in turbidity due to sediment runoff or algal blooms), oxygen depletion (common at sites that experience high rates of oxygen consumption following algal blooms or the entry of drifting organic material), or heat stress (relevant in areas that experience extreme summer heat waves). Further possible stressors are desiccation and sedimentation. The species under investigation should be easy to collect and easy to keep under experimental conditions. Stress levels should be selected with regard to local conditions. The best response variables would be those allowing the estimation of effects on short time scales like respiration rates, photosynthesis rates, chlorophyll contents, filtration rates, growth rates (in fast growing organisms), and the production of heat shock proteins or other molecular markers. Further options are reproduction and survival rates, but they most often require longer studies and may integrate also over the entire life history of the organisms under investigation.

Figure 2: Outdoor set-up used for the manipulation of light availability for macroalgae. Coquimbo, Chile 2007. Photo: Christian Pansch

Individuals collected at different sites will be kept under controlled conditions for short period (acclimatization phase) and then one group will be exposed to enhanced stress while the other serves to test for the effects of the overall experimental conditions (baseline). Control conditions should reflect long-term average values of relevant environmental parameters, while the stress group should be subjected to conditions equivalent to extreme events. Both groups will be replicated according to the expected effect size and the unexplained variation in the study system, which can be determined in pilot studies with a low replication. Experimental duration should also reflect natural regimes and can therefore range from hours to weeks. With regard to these aspects we can refer to all the experiences which have been made in the previous GAME project on stress resistance.

Each team should, if possible, identify one species that is native at their station, but invasive at another, and a further species that is invasive there but native elsewhere. Results will then be compared across stations by the end of the project. For Diploma or Master theses it might be necessary to exchange data sets between teams, so that students can compare the performance of species in their native and invasive range in one analysis.

The experiments mentioned can be supplemented by a further study that will provide additional information about invasion processes in the sea. First, the students can test whether a stressful passage, i.e. in a ballast water tank or as fouling biota on a ship hull, will lead to the selection of stress tolerant genotypes in founder populations. For this, individuals of a given native species need to be exposed to stressful conditions that will lead to partial mortality among the test organisms. In the following, the surviving individuals will be exposed to another abiotic stressor and their performance under stress will be compared to that of a random sample of the natural population.

Figure 3: Two invasive species in the European Wadden Sea. The pacific oyster *Crassostrea gigas* and the red seaweed *Gracilaria vermiculophylla*. Photo: Mark Lenz

For experiments with sessile organisms, it could be useful to deploy settlement panels at different sites prior to the start of the study to obtain specimens of, e.g., barnacles, which can then be easily transferred to the laboratory.

Summary:

Organisms: benthic invertebrates and macrophytes

Stressors: desalination, sedimentation, desiccation, oxygen depletion, low-light stress, or heat stress

Response variables: growth rates, photosynthesis rates, respiration rates, heat shock protein production, and/or survival.

Statistical analysis: ANOVA with two factors: Factor 1: Site with two levels (native/introduced); Factor 2: Stress with two levels (stressed/unstressed).

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