



Patterns and mechanisms of dispersal in a keystone seagrass species



Marlene Jahnke^a, Asbjørn Christensen^b, Dragos Micu^c, Nataliya Milchakova^d,
Murat Sezgin^e, Valentina Todorova^f, Stefan Strungaru^g, Gabriele Procaccini^{a,*}

^a Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Napoli, Italy

^b Technical University of Denmark, National Institute of Aquatic Resources, Jægersborg Allé 1, 2920 Charlottenlund, Denmark

^c National Institute for Marine Research and Development "Grigore Antipa", 900581 Constanța, Romania

^d The A.O. Kovalevsky Institute of Marine Biological Researches, 299011 Sevastopol, Russia

^e Sinop University, Faculty of Fisheries, Department of Marine Biology and Ecology, TR57000 Sinop, Turkey

^f Institute of Oceanology, P.O. Box 152 9000, Varna, Bulgaria

^g Alexandru Ioan Cuza University, Faculty of Biology, Department of Biology, Bd. Carol I 11, 700506 Iași, Romania

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ABSTRACT

Mechanisms and vectors of long-distance dispersal remain unknown for many coastal benthic species, including plants. Indications for the possibility for long-distance dispersal come from dispersal modelling and from genetic assessments, but have rarely been assessed with both methods. To this end, we assessed dispersal of the seagrass *Zostera noltei*, an important foundation species of the coastal zone. We investigate whether small scale seed dispersal and long-distance propagule dispersal do play a role for meta-population dynamics, using both genetic assessments based on eight microsatellite markers and physical modelling of ocean currents. Such assessments enhance our understanding of the biology and population dynamics of an important coastal foundation species. They are relevant for large scale conservation strategies as they give insights in the maintenance of genetic diversity and connectivity that may enhance resilience and resistance to stresses associated with seagrass loss.

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1. Introduction

Quantifying connectivity in marine populations is a crucial component of the management and conservation of coastal ecosystems (Ruiz-Montoya et al., 2015). Connectivity may confer populations resilience to anthropogenic impact and climate change (Andrello et al., 2015), and changes in patterns of connectivity may affect population persistence, leading to decline and extinction. Habitat loss and fragmentation are among the main causes of population isolation, and further changes in connectivity may represent major threats to all levels of biodiversity (Fahrig, 2003).

Connectivity among populations can be assessed using genetic approaches or modelling movements of dispersal units. In the marine environment, passive dispersal vehicles such as planktonic larvae of benthic organisms or vegetative and sexual propagules of

marine plants disperse with the movement of marine currents in which they occur (Thiel and Gutow, 2005). Genetic assessments are the most straight-forward way to assess realized connectivity, which is the result of dispersal, recruitment success and selection pressures (Sanford and Kelly, 2011). Modelling approaches in contrast can give information on dispersal potential and patterns. Comparing genetic and physical connectivity assessments can be especially useful for discerning the main modes of dispersal as well as relevant time scales (White et al., 2010). With the increasing availability and coverage of operational hydrodynamic models, semi-realistic Lagrangian modelling of physical-biological interactions has become feasible for a wide range of species, the accuracy being limited by uncertainty in the knowledge of the species biology. Recent examples include eco-regionalization in the Mediterranean basin (Serra et al., 2010; Berline et al., 2014), understanding of elusive eel recruitment aspects (Bonhommeau et al., 2009) and physical-biological interaction in spatial fish population models (Christensen et al., 2013). While most oceanographic current assessments are in the range of days to months, genetic

* Corresponding author.

E-mail address: gpro@szn.it (G. Procaccini).

structure is the consequence of the level of gene flow over many generations (Benzie, 1999). Genetic diversity can therefore give information on long-lasting barriers to dispersal. On the other hand, recent gene flow (first and second generation migrants) can also be detected with genetic assignment tests (Wilson and Rannala, 2003; Paetkau et al., 2004).

Here we assess genetic and physical connectivity of the seagrass *Zostera noltei* (Hornemann, 1832), a temperate seagrass inhabiting mainly intertidal zones of the Northern hemisphere. *Zostera noltei* is monoecious (Ackerman, 2006) and, as all seagrasses, reproduce both sexually and asexually. Sexual reproduction is thought to be common, forming dense seed banks in some meadows (Diekmann et al., 2005; Zipperle et al., 2011), but other meadows are highly clonal with little sexual reproduction (Ruggiero et al., 2005). Dispersal of the filamentous hydrophilous pollen is most likely limited to a spatial scale of metres (McMahon et al., 2014). Flowering begins with the development of a long erect generative shoot from a vegetative shoot (Loques et al., 1988). Each generative shoot may have 2–8 spathes (Loques et al., 1988) and each single spathe groups an equal proportion of male and female flowers (Loques et al., 1988; Zipperle et al., 2009). The overall process of flowering and fruiting lasts somewhere around 47 days (Alexandre et al., 2006 for *Z. noltei* in Ria Formosa Portugal), but may differ depending on the local climate. More than half of this time is required for formation and maturation of the fruits (Alexandre et al., 2006). The elongated seeds are 2–4 mm long (Loques et al., 1988; Orth et al., 2006) and are negatively buoyant, leading to very local dispersal (cm to m) as currents and waves transport the seeds in the bottom boundary layer (Berković et al., 2014; Ruiz-Montoya et al., 2015). Seeds can however remain attached to floating spathes, possibly enabling long distance dispersal and connectivity (Berković et al., 2014). The floating spathes are influenced by oceanic currents as well as local wind forcing and have the potential to travel for thousands of kilometres (Berković et al., 2014; Ruiz-Montoya et al., 2015). Long distance dispersal by floating shoots (both sexual and asexual propagules) has been investigated only recently in *Zostera* spp., claiming that sexual and vegetative floating shoots may have a major impact on meta-population connectivity, being viable even after up to 55 days of detachment (Harwell and Orth, 2002; Källström et al., 2008; Berković et al., 2014; Stafford-Bell et al., 2015). Moreover, dispersal by herbivorous animals has also been shown (Loques et al., 1988; Sumoski and Orth, 2012) and, although occasional, it may represent a significant source of connectivity between distant localities. It has been argued that in terrestrial plants such occasional nonstandard dispersal may be the main factor for long-distance connectivity among populations (Higgins et al., 2003).

Seagrasses are important foundation species providing habitat for many associated species and fulfilling important ecosystem services in the coastal zone. Inhabiting highly impacted coastal areas, the functional extinction of some species (e.g. Jorda et al., 2012 for *Posidonia oceanica*) has been forecasted for the near future. Within the Black Sea, *Z. noltei* has experienced drastic declines over the last 40 years, mainly due to pollution and eutrophication (Milchakova, 1999; Surugiu, 2008). Although cumulative human impact decreased in the Black Sea over the last few years (Halpern et al., 2015), it remains nevertheless a highly impacted sea (Halpern et al., 2008) and fragmentation of population may further increase. Given the observed decline of *Z. noltei* in many parts of the Black Sea and in other regions within its distributional range, it is crucial to understand the level of connectivity among populations. Here we assess populations of *Z. noltei* in the Black Sea at a reciprocal distance ranging from dozens to hundreds of kilometres and combine genetic structure and connectivity analyses with physical connectivity assessments to discern whether local dispersal by

seeds or long-distance dispersal by floating shoots (both sexual and asexual fragments) explains observed population structure. In the former case, the expectation is to find high genetic structure and lack of connectivity between meadows. In the latter case, genetic differentiation should be lower among populations that are predicted to be physically connected and it should be possible to detect recent migrants. If asexual propagules play an important role, we would moreover expect to find identical clones at different sampling locations.

2. Materials and methods

2.1. Study region and sampling

The study was carried out within the coastal area of the North-Western Black Sea spanning 3.5 degrees of latitude, 8 degrees of longitude and four countries. Samples were collected in eleven populations at eight sites (Fig. 1) at distances ranging from ca. 2–680 km. At each location, ca. 50 individual shoots were sampled at a reciprocal distance of 1–1.5 m (see Appendix S1 in Supporting Information for further details).

2.2. DNA extraction, microsatellite amplification and data analysis

DNA extraction and microsatellite amplification was performed as in Jahnke et al. (2015b), using eight polymorphic microsatellites (Coyer et al., 2004a). See Appendix S1 for information regarding data quality control. Multilocus genotype (MLG) identification was done for each population separately as well as combining all populations to investigate clone sharing using the software GenClone (Arnaud-Haond and Belkhir, 2007). Genotypic richness was calculated for each site according to Dorken and Eckert (2001). GenAEx ver. 6.5 (Peakall and Smouse, 2012) was used to calculate the number of alleles per locus, polymorphism and expected and observed heterozygosity. The STANDRICH package (<http://www.ccmr.ualg.pt/maree/software.php?soft=sarich>) was used to calculate standardized allelic richness (A). Arlequin (Excoffier and Lischer, 2010) was used to calculate pairwise F_{ST} among populations, while SMOGD (Crawford, 2010) was used to calculate Jost's D_{EST} (Jost, 2008). Geographic distance between sampling locations was measured using the shortest path over the sea without crossing land using Google Earth (<https://earth.google.co.uk/>). Isolation by distance (IBD) was tested using Pearson's product-moment correlation between geographic and genetic distance in R (R Development Core Team, 2014). STRUCTURE (Pritchard et al., 2000) was used to identify population clusters. Given high and significant F_{ST} values, runs were performed under assumptions of no admixture and independent allele frequencies (Falush et al., 2003). Adegenet (Jombart, 2008) for R (R Development Core Team, 2014) was used to perform discriminant analysis of principal components (DAPC) (Jombart et al., 2010), with the number of principal components set to 7, following alpha-score indication. The program BayesAss (Wilson and Rannala, 2003), a Bayesian clustering algorithm that uses Markov chain Monte Carlo (MCMC) sampling to make inferences about levels of migration and population inbreeding, was used to estimate rates of first and second generation migrants. Migration rates were also calculated based on rare alleles (Slatkin, 1985) in Genepop version 4.2 (Raymond and Rousset, 1995), which only takes into account the frequencies of uncommon alleles to calculate migration rates. For confirmation, we calculated N_m also according to Alcalá et al., 2014 using the package diveRsity (Keenan et al., 2013) in R 3.2.2 (R Development Core Team, 2014). See Appendix S1 for a detailed description of the STRUCTURE and BayesAss analyses.

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