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Zonation patterns and interspecific relationships of fucoids in microtidal environments

Luisa Mangialajo [a,b,*], Mariachiara Chiantore [b], Marie-Lucie Susini [a], Alexandre Meinesz [a], Riccardo Cattaneo-Vietti [b], Thierry Thibaut [a]

[a] Université de Nice-Sophia Antipolis, EA 4228 ECOMERS, Parc Valrose, F-06108 Nice cedex 2, France
[b] Dip.Te.Ris., Università degli Studi di Genova, C.so Europa 26, I-16132 Genova, Italy

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ABSTRACT

The Northwestern Mediterranean Sea is a microtidal system, where barometric pressure and local wave exposure play the paramount role in sea water level variation. Herein, *Cystoseira amentacea* var. *stricta* and *Cystoseira compressa* are common species, generally co-occurring on exposed shores where they form a fucoid belt that characterise a narrow area called the infralittoral fringe.

To better understand the eventual zonation patterns and the interspecific relationships of *Cystoseira* species, a multi-response manipulative experiment based on cross-transplantation, was set up. The fitness of the two species was assessed in terms of survival, growth and reproductive conditions; the role of a given *Cystoseira* and of the presence of a hard to measure environmental gradient was assessed on the recruitment of the two species and on the composition of assemblages re-colonising the bare substrate.

Our results highlight a different response to the manipulation of the two species: while *C. compressa* fitness does not seem to be affected by the vertical position on the shore, *C. amentacea* var. *stricta* survival, growth and reproduction change in function of the gradient. The height on the shore should therefore be taken into account for a successful restoration of lost habitats. The recruitment of the two species and the early phases of succession in re-colonisation of the substratum are also affected by the gradient, and the dispersal of both species seems to be more limited than it was assumed until now (approximately 20 cm). *C. amentacea*, able to spread in continuous belts in the infralittoral fringe, may be a better competitor than *C. compressa*, thriving at a higher level on the shore, with its lower limit potentially confined by competitive exclusion of *C. amentacea* var. *stricta*. The two *Cystoseira* species cannot be considered as ecological analogues and determinism seems to drive their distribution in the infralittoral fringe. Nevertheless, stochastic factors, and in particular the very limited dispersal, can be assumed as major factor in regulating large scale distribution of these species.

1. Introduction

In macrotidal systems, where zonation patterns are evident, different species of large brown algae of the order Fucales (fucoids) commonly dominate, forming dense stands over large areas (Menge and Branch, 2000). Such assemblages are characterised by high biodiversity, because fucoid canopies lead to "biological habitat amelioration" (*sensu* Moore et al., 2007) through the formation of three-dimensional habitats. For this reason, fucoids are considered ecosystem engineers (Jones et al., 1994), on which most other species and their communities rely (Jenkins et al., 1999; Schiel and Foster, 2006). Coexistence of fucoid species is common in the intertidal zone, yet the stochasticity of their distribution or the eventual role of environmental gradients, as much as their interspecific relationships are still little known (Chapman and Johnson, 1990; Gil Choi and Norton, 2005).

The Northwestern Mediterranean Sea is a microtidal system, where barometric pressure and local wave exposure play a paramount role in sea water level variation (Ballesteros, 1989; Ballesteros and Romero, 1988; Feldmann, 1937). The Fucales *Cystoseira amentacea* var. *stricta* Montagne (hereafter *C. amentacea*) and *Cystoseira compressa* (Esper) Gerloff and Nizamuddin are common species, generally co-occurring on exposed shores, where they characterise a narrow area (20–30 cm in height) called the upper infralittoral fringe (Pérès and Picard, 1964), that is intermittently submerged, mostly accordingly to wave action. Such assemblages are strongly submitted to sudden and important changes in environmental features (temperature, desiccation, salinity, herbivory) due to their position at the interface between sea and land. *C. amentacea* and *C. compressa* distribution is limited vertically by desiccation in their upper limit (Delgado et al., 1995)

* Corresponding author at: Université de Nice-Sophia Antipolis, EA 4228 ECOMERS, Parc Valrose, F-06108 Nice cedex 2, France. Tel.: +33 4 92076832; fax: +33 4 92076849.
E-mail address: luisa.mangialajo@unice.fr (L. Mangialajo).

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and by herbivorous fishes (Vergés et al., 2009) in the lower limit, generally few centimetres behind sea-water level. *C. amentacea* and *C. compressa* height on the shore may change at a very small scale (cm) accordingly to variable wave exposure in function of local coast morphology, as schematised in Fig. 1. For this reason, in some papers, the heterogeneity due to absolute vertical distribution of organisms in the infralittoral fringe is considered to be of the same magnitude of other sources of spatial and temporal heterogeneity (*i.e.* Menconi et al., 1999). Such environmental gradient, hardly measurable for the limited vertical extension (20–30 cm of vertical height) and the high variability in absolute height due to coastline morphology and very local wave exposure may be more important than assumed in recent papers.

C. amentacea usually forms continuous belts (Molinier, 1960), while *C. compressa* is usually found in patches on the upper limit of *C. amentacea*'s distribution, a pattern that is common for the western Mediterranean Sea. Alternative patterns are characterised by more or less discontinuous belts of *C. amentacea*, co-occurring with *C. compressa* patches, or by the only presence of *C. compressa*. These alternative patterns are often associated to a general higher level of human-induced disturbance (sedimentation, eutrophication, historical use of the coastline, terrestrial inputs).

In this work, a multi-response manipulative experiment, based on cross-transplantation of the two *Cystoseira* species, was set up. In a deterministic perspective, effects of the vertical gradient on survival, growth, reproduction, recruitment and organisms colonisation of bare substratum, are expected in the cross-transplanted condition. Contrarily, no differences are expected in fitness of the two species and in the early phases of succession, being the distribution patterns mostly linked to stochastic processes.

2. Methods

2.1. Study area

The multi response manipulative experiment was carried out in Bogliasco near Genoa (Ligurian Sea, Western Mediterranean, Fig. 1). Herein, the Northwestern Mediterranean common pattern is present: *C. amentacea* forms a continuous belt (*C. amentacea* zone: ZCA), while *C. compressa* is found in patches on the upper limit of *C. amentacea*'s distribution (*C. compressa* zone: ZCC).

2.2. Experimental setup

The experiment was set up in order to assess (1) the fitness of the two species inside their own and the reciprocal zone, in terms of survival, growth, reproductive conditions (presence of fertile conceptacles) and (2) the recruitment and the re-colonisation of bare substratum, in function of the presence of a given *Cystoseira* species and of the vertical environmental gradient at the small scale (centimetres).

The experiment started between March 30 and April 15 2004, applying a transplantation technique whose feasibility and efficiency had already been tested (Susini et al., 2007). The technique is made of three phases: clearing of all plots (1600 cm^2 each), drilling the rock (5 holes 18 mm diameter in each plot) and transplanting an individual plant in each hole, with the aid of epoxy putty (IVEGOR); in this last phase, particular attention was paid to hydrodynamic conditions, both during the manipulation and in the first 24 h following manipulation, the time necessary for catalysation of epoxy putty, a crucial step for a successful transplantation. Due to the transplantation technique (drilling the rock and using epoxy putty), it was not reasonable to transplant more than five plants per plot and therefore it was not possible to reproduce the natural density of individuals (especially for *C. amentacea*, a caespitose plant whose holdfasts can cover more than 30% of the substrate, Mangialajo et al., 2008).

Three different sites, a few hundreds of metres apart, were chosen on natural rocky shore. For each site, 6 random plots within the ZCA and 6 plots within the ZCC were scraped to bare rock, for a total of 36 plots. Two interspersed plots/site (Fig. 1) were devoted to the Transplantation (T) of each species in its own zone (*C. amentacea*/ZCA and *C. compressa*/ZCC) and two to the Cross Transplantation (CT) of the two species (*C. amentacea*/ZCC and *C. compressa*/ZCA). Two remaining plots per site in each zone were kept untouched and used as controls (No Transplantation, NT) for the study of recruitment of the two species (see below) and re-colonisation of bare substratum. The corners of each plot were marked with epoxy putty and marks were maintained throughout the experiment.

As response measures for testing the fitness of the two species in each zone, we considered the survival rate, the growth and the reproductive conditions. Survival rates of the transplanted and cross-transplanted individuals were assessed on May 15, June 29, July 30, November 25, 2004 and March 17, 2005, by counting vital individuals in each plot. The growth of both species was assessed on June 29, 2004, nearly three months after manipulation, during maximum growth period for these species (Barceló et al., 2000). The length of 5 randomly chosen primary ramifications was measured in each plot. As control, the same amount of randomly chosen individuals of the same species was measured in nearby non-manipulated assemblages. Also, reproductive conditions were assessed on June 29, 2004, in the reproductive period of both species. Three apical portions of each species were randomly sampled in each manipulated plot. As control, the same amount of apical portions was randomly sampled in nearby non-manipulated assemblages.

Recruitment and dispersal were assessed on March 2005, being the reproductive period of both species from April to November (Barceló et al., 2000). In large brown seaweeds, mortality during early-life stages can be very high and potentially linked to several physical and biological factors (Schiel and Foster, 2006). We chose to quantify the recruitment after a year, when recruits measure at least 1 cm and are relatively easily to detect and identify in the

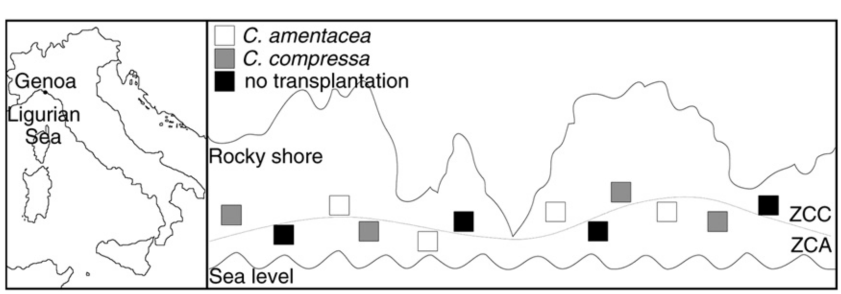

Fig. 1. A) Location of the experiment: Genoa, Ligurian Sea. B) Schematic representation of the set up of the experiment in one out of the three sites. The dotted line represents the theoretical separation between the two zones: ZCA (*Cystoseira amentacea* zone) and ZCC (*C. compressa* zone). It is deliberately irregular, accordingly to the coastal morphology. In each site 6 plots were scraped in the *C. amentacea* zone (below the dotted line) and 6 in the *C. compressa* zone (above the dotted line). Two interspersed plots were assigned to each treatment (*C. amentacea* transplanted, *C. compressa* transplanted, no transplantation).