



## Carry over effects of nutrient addition on the recovery of an invasive seaweed from the winter die-back



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### ABSTRACT

Nutrient enrichment of coastal waters can enhance the invasibility and regrowth of non-native species. The invasive alga *Caulerpa cylindracea* has two distinct phases: a well-studied fast-growing summer phase, and a winter latent phase. To investigate the effects of nutrient enrichment on the regrowth of the seaweed after the winter resting-phase, a manipulative experiment was carried out in intertidal rockpools in the North-western Mediterranean. Nutrients were supplied under different temporal regimes: press (constant release from January to May), winter pulse (January to March) and spring pulse (March to May). Independently from the temporal characteristics of their addition, nutrients accelerated the regrowth of *C. cylindracea* after the winter die-back, resulting in increased percentage covers at the peak of the growing season. Nutrient addition did not influence the number and length of fronds and the biomass. Native components of the algal community did not respond to nutrient additions. Our results show that nutrient supply can favour the spread of *C. cylindracea* even when occurring at a time of the year at which the seaweed is not actively growing.

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### 1. Introduction

The introduction and spread of non-native species is globally acknowledged among the causes of alterations in the biodiversity and functioning of natural ecosystems globally (Mack et al., 2000; Pimentel et al., 2000). The potential for non-native species to establish and spread outside of their native range is often related, among other factors, to the level of disturbance that characterizes recipient systems (Burke and Grime, 1996; Hobbs and Huenneke, 1992) and on the biology of the invasive species (Leung and Mandrak, 2007). Many invaders are opportunistic species that can readily take advantage of enhanced resource availability in the non-native range due to increases in supply or reduced uptake by native species following a disturbance (Davis et al., 2000; Lohrer et al.,

2000). Eutrophication of water in coastal environments from anthropogenic activities has increased in the last two decades (DeBruyn and Rasmussen, 2002; McClelland and Valiela, 1998), causing significant alterations to benthic and pelagic ecosystems (Bokn et al., 2003; Burkholder et al., 2007; Hillebrand, 2003; Hughes et al., 1999; Micheli, 1999; Worm et al., 2000). Enhanced nutrient loading can favour the establishment and spread of non-native species by conferring invaders a competitive advantage over native competitors (Incera et al., 2009; Sánchez and Fernández, 2006), and through the degradation of native communities (Atalah and Crowe, 2010; Balata et al., 2010; Stimson et al., 2001; Torres et al., 2004). Nutrient enrichment is generally constant in urban areas (i.e., eutrophic conditions) and, to date, most studies have considered nutrient enrichment as a press disturbance. However, inputs along less developed coastlines are generally linked to river run-off (Bonsdorff et al., 1997; Justić et al., 1995; Turner and Rabalais, 1994) and, hence, characterized by large temporal variation. Thus these environments are more likely to experience pulse rather than press events. Because of the more

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stochastic nature of nutrient delivery to these systems, we may expect the response of native and non-native species to vary according to the timing of their release. Positive effects in invasive algae may occur when nutrients become available at times of the year at which non-native species are able to uptake and use them more readily than extant native species.

Seaweeds are among the most noxious invaders in coastal environments (Gribben et al., 2013; Maggi et al., 2015; Schaffelke and Hewitt, 2007; Williams and Smith, 2007; Wright and Gribben, 2008). Correlative and experimental studies have shown that nutrient inputs often enhance their establishment and spread (Ceccherelli and Cinelli, 1997; Ceccherelli and Sechi, 2002; Gennaro and Piazzzi, 2011; Piriz et al., 2003; Steen and Scrosati, 2004; but see Vaz-Pinto et al., 2014 as an example of less efficient uptake than native counterparts) and many of these opportunistic invasive algae can store nutrients in their tissues to sustain growth in periods when they are in short supply (Fong et al., 2004; Gennaro et al., 2015). Moreover, differences in the storage capacity among species may contribute to shape the structure of macroalgal assemblages. For instance, Fujita and Goldman (1985) found that greater N uptake during periods of high availability, allowed *Gracilaria tikvahiae* to sustain its growth longer than *Ulva lactuca* and *Enteromorpha* spp. in N-free medium. In addition, N uptake in macroalgae is less sensitive to temperature than growth (Duke et al., 1989) and winter uptake rates - a time of low algal growth - can be as high as those occurring during summer months (Pedersen et al., 2004). Thus, the ability to efficiently uptake and store nutrients during pulses of release throughout the year may explain the success of some non-native seaweeds.

The invasive green seaweed, *Caulerpa cylindracea*, (previously *Caulerpa racemosa* var. *cylindracea*) is among the most widespread invasive species in the Mediterranean Sea (Piazzzi and Balata, 2009; Renoncourt and Meinesz, 2002). *C. cylindracea* does appear to be N-limited in its invasive range and the positive effects of nutrient enhancement on its growth (Gennaro and Piazzzi, 2011, 2014) are likely the result of its tolerance to hypertrophic conditions and an ability to quickly uptake and store nutrients in its coenocytic thallus (Gennaro et al., 2015). Positive effects of nutrients enhancement have been documented in summer for *C. cylindracea*, when this seaweed is actively growing (Gennaro and Piazzzi, 2011; Gennaro et al., 2015). However, in the Mediterranean Sea, *C. cylindracea* alternates a fast-growing phase during summer (Ceccherelli et al., 2002; Piazzzi and Balata, 2009) with a latent phase during winter, characterized by loss of fronds and ramuli (Ruitton et al., 2005). To the best of our knowledge, no study has assessed how the supply of nutrients outside of the period of active growth influence the competitive ability of *C. cylindracea* in respect to that of native components of macroalgal assemblages. Similarly, no known study has studied how nutrient input in small long-lasting increases (press) promotes regrowth when compared to a sudden increase in them (pulse).

Here, we experimentally evaluated how nutrient input regimes differing in timing and duration (but not intensity) influenced the dynamics of *C. cylindracea* in intertidal rockpools.

In particular, we predicted that: (1) if *C. cylindracea* is able to uptake and store nutrient during the declining phase, nutrient addition in winter (January to March) would reduce its regression and/or promote an earlier recovery during the spring re-growing phase, thus resulting in a greater summer peak abundance if carry over effects are long lasting; (2) if *C. cylindracea* is able to uptake and store nutrient during the resting phase, nutrient addition during this phase (March to May) would promote an earlier recovery during the spring re-growing phase and enhance summer peak abundance even if carry over effects are short lasting; (3) if *C. cylindracea* is able to uptake and store nutrient throughout the

declining – regrowing phase, a continuous nutrient addition (Press) during that period would reduce the winter regression, promote an earlier recovery during the spring re-growth and enhance summer peak abundance even if carry over effects are short lasting. Finally, we predicted that (4) the ability of *C. cylindracea* to take advantage of nutrient inputs would be greater than that of native macroalgae, irrespective of the temporal regime.

## 2. Materials and methods

This study was conducted in rockpools along an exposed sandstone rocky shore, approximately 5 km south of Livorno (Calfuria, 43°47'N, 10°33'E) on the North-West coast of Italy. Nutrient manipulation took place from January to May 2016. Native assemblages were composed by algal stands of *Cystoseira compressa*, *C. brachycarpa* var. *balearica* and *Halopteris scoparia*, small-sized filamentous forms (such as *Ceramium* sp.), coarsely branched (*Gelidium* sp.) and articulated coralline algae (*Corallina elongata*, *Jania* sp.). Pools supported a dense population of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* (Benedetti-Cecchi and Cinelli, 1992) while sessile invertebrates, such as the tube-forming gastropod *Vermetus triquetter*, serpulids and the barnacle *Balanus glandula*, were rarely found (Incera et al., 2010; Maggi et al., 2012). All rockpools were colonised by *Caulerpa cylindracea* (Incera et al., 2010).

### 2.1. Experimental design

A total of 12 rockpools with a similar wave exposure were randomly selected along a 0.7 km stretch of coast in order to reduce as much as possible variability among rockpools (Maggi et al., 2012). These were selected based on a previous pilot study survey, in order to have similar mean surface area ( $6.5 \pm 3.5$  m<sup>2</sup> SE) and depth ( $46.5 \pm 15.1$  SE cm), as well as similar native communities and initial *C. cylindracea* percentage cover. This resulted in a relatively low number of available rockpools (similarly to Maggi et al., 2012). Five 15 × 15 cm quadrats were randomly identified in each rockpool and marked by applying epoxy putty (Subcoat S, Veneziani) on the two upper vertices of each quadrat. Rockpools were randomly assigned to one of four nutrient enrichment treatments (three rockpools per treatment): (1) control, no nutrient addition; (2) pulse addition of nutrients from January to March (3) pulse nutrient addition from March to May; (4) press nutrient addition from January until May. Nutrients were enhanced by deploying two 20 × 5 × 5 cm nylon mesh bags, each containing either 100 g, for the pulse treatments, or 50 g for the press treatment of fertilizing pellets (Osmocote®, NPK 17-11-10) about 20 cm from each quadrat. Nutrient bags were checked regularly every two to three weeks and replaced as soon as possible to ensure a consistent nutrient enrichment. Previous studies have shown no artefacts of mesh bags (Gorgula and Connell, 2004; Bulleri et al., 2012) and, therefore, we did not establish procedural controls. In order to estimate the amount of nutrients released from the nutrient bags, pellet dry weight was analysed upon mesh bag retrieval and compared to pre-deployment weight. Nutrient dissolution rate was twice as high for the January Pulse ( $6.35 \pm 1.23$  of N and  $4.11 \pm 1.23$  g/day · m<sup>2</sup> of P) and March Pulse ( $8.01 \pm 1.29$  of N and  $5.18 \pm 0.84$  g/day · m<sup>2</sup> of P) compared to the Press treatment ( $3.16 \pm 0.36$  of N and  $2.04 \pm 0.23$  g/day · m<sup>2</sup> of P, Fig. A1).

### 2.2. Sampling and analyses of data

The percentage cover of *Caulerpa cylindracea* and that of resident algal species was visually estimated using 15 × 15 cm plastic frames subdivided into 16 sub-quadrats. A score from 0 to 4% was

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