

**A tale of two invaders: divergent spreading kinetics of the alien green algae *Caulerpa taxifolia*  
and *Caulerpa cylindracea***

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## **Abstract**

The two alien green algae *Caulerpa taxifolia* and *Caulerpa cylindracea* (formerly *Caulerpa racemosa* var. *cylindracea*) are among the most notorious and threatening invasive species in the Mediterranean Sea. From the beginning of their introduction, *C. taxifolia* aroused a great concern due to its initial exponential spread and impacts on native ecosystems, whilst *C. cylindracea* received lower attention. In this paper, the distribution of the two aliens over the last 30 years in the Italian side of the Ligurian Sea (NW Mediterranean Sea) is reviewed and the kinetics of their spreading is compared. We combined available data on habitat occupancy with data on substratum cover obtained during underwater surveys to compute the average annual spreading rates for both aliens. *C. taxifolia* had an impressive expansion phase from 1984 to 2000 but then, its dispersal rate showed lower than that predicted and the species did not persist in areas formerly colonized. Today, abundance of this species is strongly declined as it disappeared from most of the attained areas. On the contrary, *C. cylindracea* exhibited an impressive and constant expansion from the beginning of its first appearance in the Ligurian Sea and, today, it is still increasing its range and habitat occupancy. Its abundance results 1.5-times greater than that reached by *C. taxifolia* during the period of its maximum expansion. The divergent kinetics of spreading of the two aliens prevents any possibility of generalization of the future behaviour of invasive species in the Mediterranean Sea, and continuous and periodic surveys are thus mandatory to understand the kinetics of expansion and to define species-specific models.

**Keywords:** *Caulerpa taxifolia*; *Caulerpa cylindracea*; bioinvasion; kinetics of spreading; Ligurian Sea; Mediterranean Sea.

## Introduction

The incessant increase of human footprint and climate change favoured invasion by non-indigenous species (hereafter NIS) introduced by human activities worldwide (Occhipinti-Ambrogi 2007; Jauni et al. 2015). Invasive NIS are recognized as one of the major drivers of biodiversity change across the globe and may have negative effects on the health of native ecosystems (Piazzi and Balata 2008; Vilà et al. 2011) and on the provisioning of ecosystem processes and services (Katsanevakis et al. 2014). Kinetics of biological invasions has been largely investigated in terrestrial ecosystems (Buckley et al. 2007; Blackburn et al. 2011; Vilà et al. 2011) and, despite the growing number of well-documented invasions in marine systems (Carlton 1996), comparatively little is known about the mechanisms underlying the success or failure of invasion (Stachowicz et al. 2002) and the possible models followed by the kinetics of their spreading (Boudouresque and Verlaque 2012). Investigations dealing with the behaviour of marine NIS, spanning long time periods and large spatial scales, are rather uncommon (Occhipinti-Ambrogi and Sheppard 2007).

The Mediterranean Sea is one of the seas of the world mostly affected by biological invasions (Occhipinti-Ambrogi 2007), both in terms of the length of time that NIS have been present and in number of species detected, with nearly 900 NIS recorded (Galil 2009; Zenetos et al. 2010; Galil et al. 2014). The most notorious and threatening invasive events thrived by algae in the Mediterranean Sea are probably represented by the two alien green algae *Caulerpa taxifolia* (Vahl) C. Agardh and *Caulerpa cylindracea* (Sonder), both exhibiting among the fastest spread rates of any marine bioinvasions (Meinesz et al. 2001; Ruitton et al. 2005). *Caulerpa cylindracea*, formerly recognized as *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque (Verlaque et al. 2003), has been recently identified as an independent species distributed in Australia, Indonesia, New Caledonia, Canary Islands and the Mediterranean Sea (Belton et al. 2014).

*C. taxifolia*, native to the Caribbean Sea, was accidentally released from the Oceanographic Museum at Monaco into the Mediterranean Sea in 1984 (Meinesz and Hesse 1991), where it rapidly became a dominant feature in the northwestern Mediterranean coastline (Meinesz et al. 2001),

spreading along 190 km of coasts of 7 countries: Croatia, France, Italy, Monaco, Spain, Tunisia and Turkey (Jaubert et al. 2003). In Italy, *C. taxifolia* mainly spread along the western coast of Liguria since 1992 (Meinesz et al. 2001). Thanks to its expansionistic success (De Villèle and Verlaque 1995), mostly due to an extremely efficient vegetative propagation, an amazing adaptability to a new environment and a weak pressure from grazers, *C. taxifolia* was considered a strong invader (Montefalcone et al. 2010a) and one of the main threat to benthic native communities (Glasby 2013). *C. taxifolia* had been listed as one of the top 100 worst NIS on earth (IUCN The World Conservation Union, available at: <http://www.issg.org/database>), so that it was usually identified with the nickname of ‘killer alga’ (Meinesz 1999). From the beginning of its introduction in the Mediterranean Sea, scientists hypothesized an exponential spread by a factor 6 annually (Boudouresque et al. 1995), culminating in an estimated surface affected of more than 8,000 ha by 2000 (Jousson et al. 2000) and 30,000 ha by 2002 (Withgott 2002).

*Caulerpa cylindracea* was observed for the first time in 1990 along the coasts of Libya (Verlaque et al. 2003). It was initially viewed as a Lessepsian migrant from the Red Sea but, recently, its southwestern Australian origin has been proved (Verlaque et al. 2003; Belton et al. 2014). Although this NIS received lower attention with respect to *C. taxifolia*, it exhibited an impressive spread across the Mediterranean Sea where it colonized the coasts of 12 countries: Albania, Algeria, Croatia, Cyprus, France, Greece, Italy, Lybia, Malta, Spain, Tunisia and Turkey (Klein and Verlaque 2008). In Italy, *C. cylindracea* colonized the coasts of Tuscany and several sites of Liguria since 1996 (Bussotti et al. 1996). Ship traffic and aquaria imports can be considered as the main vectors. Since its first appearance in the western Mediterranean basin, this alga had been showing an incessant expansion because of its fast propagation and because it is not affected by competitive interactions with *C. taxifolia* or other turf-forming algae (Piazzi and Ceccherelli 2002; Piazzi et al. 2003). *C. cylindracea* was considered a very strong invader (Montefalcone et al. 2010a) and it had been included in the list of the 100 worst NIS of the Mediterranean Sea (Streftaris and Zenetos 2006). Due to its high acclimative capabilities (Raniello et al. 2006), *C. cylindracea* showed a wider range

of colonized areas than *C. taxifolia*, occurring in the whole basin and out-competing with native communities such as other algae (Verlaque and Fritayre 1994; Verlaque et al. 2000; Piazzini et al. 2003) and seagrass (Ceccherelli et al. 2002). *C. cylindracea* has a high adaptability to physical and abiotic factors and may spread on all types of substratum, in sheltered and exposed areas, at depths ranging from the intertidal zone down to 90 m (Argyrou et al. 1999; Žuljević et al. 2003; Capiomont et al. 2005) and both in disturbed and pristine habitats (Boudouresque and Verlaque 2012).

For *C. taxifolia* regular cartographies have been elaborated to monitor its expansion, especially for the period between 1984 and 2000 (Gravez et al. 2001). On the contrary, available data on the abundance of *C. cylindracea* are uncommon and are often imprecise. Only maps reporting the occurrence of this NIS have been compiled, where the length of the coastline affected can be roughly estimated (see for instance Gravez et al. 2001; Belsher et al. 2003; Klein and Verlaque 2007; Ruiz et al. 2011; <http://www.ciesm.org/atlas/appendix4.html>).

The spread of a NIS can be expressed as either surface (in ha or m<sup>2</sup>) or length of the coastline (in km) colonized, whilst its abundance can be expressed by substratum cover (%). The surface colonized by a NIS is usually estimated as a semi-quantitative measure of the total area affected by invasion (defined either as ‘habitat occupancy’ or ‘surface attained’), and then expressed as classes of abundance (Meinesz et al. 1998). Reports on the occurrence of *C. taxifolia* and *C. cylindracea* in Liguria are available from the Italian database on benthic marine species census, which expressed their abundance as classes (Meinesz et al. 1998), and in a number of scientific papers and grey literature. Although comparatively less available, data on substratum cover may be assessed during scuba diving surveys adopting one of the methodology proposed to estimate cover (Montefalcone 2009), all allowing for a quantitative measure of the abundance of the two NIS over a fixed area (Bianchi et al. 2004).

In this paper the spread of the two invasive NIS *C. taxifolia* and *C. cylindracea* over the last 30 years in the Italian side of the Ligurian Sea, which is the northernmost and coldest sector of

expansion reached by both species in the NW Mediterranean Sea, is reviewed. We combined available data from the literature on abundance for both NIS, expressed as habitat occupancy, with data obtained during underwater surveys and expressed as substratum cover. The kinetics of the spreading of both NIS in the Ligurian Sea has been evaluated by computing their annual spreading rates, which have been compared with the spreading rates hypothesised at the beginning of their expansion in order to verify whether the present day situation is similar to what had been predicted during the first stages of the invasion or whether predictions went wrong.

## **Materials and methods**

Reports on occurrence and habitat occupancy of *Caulerpa taxifolia* and *Caulerpa cylindracea* along the 300 km coastline of Liguria, an administrative Region of NW Italy (Mediterranean Sea), were collected from personal archives, available literature, an Italian database on benthic marine species census ([http://www.progettomac.it/specie\\_censite.asp](http://www.progettomac.it/specie_censite.asp)) and from personal communication by local experts (see supporting information Table S1). Reports encompassed a total of 23 Ligurian coastal areas, 12 located in the western and 11 in the eastern Ligurian coast: Mortola (MO); Ventimiglia (VM); Ospedaletti (OS); Sanremo (SR); Imperia (IM); Diano Marina (DM); Alassio-Gallinara (AG); Ceriale (CE); Bergeggi (BE); Varazze (VA); Cogoleto-Arenzano (CA); Vesima (VS); Genoa-Foce (FO); Sturla (ST); Quarto (QA); Quinto (QI); Portofino (PO); Zoagli (ZO); Chiavari (CH); Sestri Levante (SL); Framura (FR); Monterosso al Mare (MM); La Spezia (SP) (see Fig. 1). Reports were divided in four distinct periods, which are not uniform in number of years but consistent in the total number of reports available: i) from 1984 (the year of the first release of *C. taxifolia* in the Mediterranean Sea) to 1993; ii) from 1994 to 2000; iii) from 2001 to 2008; iv) from 2009 to 2013. Inspiring to the classification proposed by Meinesz et al. (1998), three classes of habitat occupancy were considered for mapping purposes: 1) < 200 ha; 2) 200 to 2000 ha; 3) > 2000 ha.

To compute the spreading rate, the number of hectares occupied by the two NIS along the whole Ligurian coast for each period was cumulated from the raw data reported in all the sources consulted (see supporting information Table S2); when no detail was available, we conservatively assumed a number of hectares equal to 20, 200 and 2000 ha for the three classes of habitat occupancy, respectively. The annual spreading rate ( $r$ ) was obtained using the formula:

$$r = [A_n/A_{(n-1)}] \times e^{(1/y)},$$

where  $A_n$  is the number of hectares occupied by the species in the period  $n$ ,  $A_{(n-1)}$  is the number of hectares occupied by the species in the previous period and  $y$  is the number of years between the two periods, computed considering the central year of each period. Three spreading rates have been computed for *C. taxifolia*, i.e. from the first (1984-1993) to the second (1994-2000) period, from the second to the third (2001-2008) period and from the third to the last (2009-2013) period, whilst only two rates for *C. cylindracea* (from the second to the third and from the third to the last period).

Data on substratum cover (%) of the two *Caulerpa* species were rare for the first two periods, i.e. from 1984 to 2000. During the last two periods (2001-2008 and 2009-2013) scuba diving surveys have been regularly carried out in most of the above listed coastal areas of the Liguria (65% of the areas), namely MO, VM, OS, SR, AG, BE, CA, FO, ST, QA, QI, PO, SL, FR, MM. During dives, the percent cover of the two NIS has been visually estimated every 5 m by two divers independently swimming approximately 3m above the bottom on a seabed surface of about 25 m<sup>2</sup> (Montefalcone 2009), along either 100 m long and 10 m wide depth transects laid on the bottom perpendicularly to the coast from the shoreline to a maximum depth of 35 m, or 20 m long and 2 m wide Line Intercept Transects (LIT) laid parallel to the coast at various depths, typically between 10 m and 30 m (Bianchi et al. 2004). The transect's typology was chosen according to the main aim of the study, in a variable number of replicated transects according to the extent of the study area (minimum 6, maximum 30). Most of these transects were laid in correspondence of *Posidonia oceanica* meadows, as degraded areas of *P. oceanica* have been shown to represent a favourable substratum for the spreading of the two *Caulerpa* species (Montefalcone et al. 2010a; Bulleri et al. 2011), but

many were also positioned in correspondence of either sandy or rocky bottoms. For more details on field activities also refer to Peirano et al. (2005), Montefalcone et al. (2006, 2007a, 2007b, 2009, 2010a, 2010b), Giovannetti et al. (2010), Parravicini et al. (2010), Rovere et al. (2010), Vacchi et al. (2010, 2012).

Analyses of variance (2 ways-ANOVAs) were performed to test for differences in the cover values of the two *Caulerpa* species between the last two periods (i.e. 2001-2008 and 2009-2013, fixed and orthogonal) and areas (15 levels, random). As the number of underwater transects in each area was variable, analyses were performed using 6 randomly selected transects as replicates. Prior to analyses, cover values were examined for homogeneity of variances using the Cochran's test. When a treatment factor was significant, the differences between levels were determined using the Student-Newman-Keuls test (SNK test).

## **Results**

In the first period (1984-1993), *Caulerpa taxifolia* occurred only in three western areas of the Ligurian coast, namely SR, IM and DM (Fig. 1), with a habitat occupancy that never exceeded 200 ha. In the second period (1994-2000) *C. taxifolia* reached the largest expansion and abundance, colonizing virtually all the westernmost coastal areas of Liguria, from the Italian-France frontier (MO) to CE. Its habitat occupancy was always greater than 200 ha in all the areas between SR and DM, and often greater than 2000 ha (IM and DM). During this period *C. taxifolia* also colonized two easternmost areas, VA and CH, where it was reported in small stands that had been successfully eradicated. In the third period (2001-2008), the spread of *C. taxifolia* slowed down; in all the colonized areas its abundance diminished never exceeding 2000 ha. The last period (2009-2013) was characterized by a global decline in the spread and abundance of *C. taxifolia*, which disappeared from most of the original colonized areas, being reported only in the areas between VM and IM, with abundances lower than 200 ha. From 2010 *C. taxifolia* disappeared also from the area of OS.



*Caulerpa cylindracea* was absent in Liguria until 1996, the year of its first sighting in Genoa, the chief town in the centre of Liguria. During the second period (1994-2000), *C. cylindracea* started to spread in coastal areas around Genoa, from VA in the western Liguria to Quinto (QI) in the eastern coast, with habitat occupancy always lower than 2000 ha (Fig. 1). In the third period (2001-2008), *C. cylindracea* had spread toward East and West, colonizing nearly all the Ligurian coastal areas, with habitat occupancy larger than 2000 ha in some cases (BE, FO). The last period (2009-2013) was characterized by a continuous spread of *C. cylindracea*, especially along the western Ligurian coast. In many areas (23% of the areas) *C. cylindracea* attained surfaces larger than 2000 ha (AG, BE, FO, PO, MM).

*C. taxifolia* and *C. cylindracea* showed a divergent kinetics during their spread (Fig. 2). Habitat occupancy of *C. taxifolia* attained the highest value of about 8,600 ha during the second period (1994-2000), thanks to an average annual spreading rate of 1.63; then it started to decrease gradually with an annual reduction rate of 0.81 and 0.65 in the following two periods, respectively, reaching values of habitat occupancy no greater than 150 ha in the last period (2009-2013). Conversely, habitat occupancy of *C. cylindracea* increased exponentially from the second (1994-2000) to the third period (2001-2008) and from the third to the last period (2009-2013), showing annual spreading rates of 1.44 and 1.10, respectively, and reaching the highest abundance of about 12,500 ha in the last period.

In the areas of occurrence, *C. taxifolia* showed a mean cover along transects of 24% ( $\pm 2\%$  SE) during the third period (2001-2008), whilst it experienced a significant ( $p < 0.001$ , Table 1) decrease of cover values, or a disappearance, in all the attained areas during the last period (2009-2013), reaching a mean cover of 3% ( $\pm 2\%$  SE) (Fig. 3). *C. cylindracea* showed a mean cover of 23% ( $\pm 6\%$  SE) during the third period (2001-2008) and then it slightly increased to a mean cover of 30% ( $\pm 4\%$  SE) during the last period (2009-2013) (Fig. 3). Cover of *C. cylindracea* increased significantly ( $p < 0.001$ , Table 1) between the third and the fourth period only in the westernmost (namely MO,

VM, OS, SR, AG) and in the easternmost (namely PO, FR, MM) areas, which have been the last coastal areas reached during its expansion.

## **Discussion**

Boudouresque and Verlaque (2012) identified four successive phases in the kinetics of invasive species: (i) arrival, (ii) settlement, (iii) expansion, (iv) persistence. *C. taxifolia* exhibited, after its arrival and successful settlement, a rapid phase of expansion where it tried to occupy all of the habitats and the entire geographical range to which it may have access; this phase culminated with a maximum expansion reached about 12-14 years after its first introduction in the Ligurian Sea (Jousson et al. 2000; Withgott 2002). However, this species did not persist in the colonized habitats as, at the end of the expansion phase (around the 2000), its abundance naturally collapsed to a very low level. Today, only small stands of this NIS still occur in the westernmost areas of Liguria (VM, SR and IM), which are among those areas where this species reached its highest abundance in the past (Meinesz et al. 1998). In Liguria the kinetics of the invasion of *C. taxifolia* has been shown to follow the model of the ‘boom and bust’, as hypothesised by Boudouresque and Verlaque (2012).

*C. cylindracea* showed, after its arrival and successful settlement, a phase of expansion with a slightly lower growing rate than that experienced by *C. taxifolia* (i.e. 1.44 vs 1.63, respectively), but with a comparatively faster and more widespread colonization, consistent with its higher invasive potential compared to *C. taxifolia* (Piazzi et al. 2001a). *C. cylindracea* persisted and occupied all of the accessible habitats and the entire geographical range of the Liguria: after 17 years from its first introduction, it is still in the expansion phase with no sign, anywhere, of either decline or disappearance. From 1996 to 2008 the abundance of *C. cylindracea* in Liguria had been increased by more than 1-fold of magnitude and, in the last four years (from 2009 to 2013), its abundance was doubled. Habitat occupancy of *C. cylindracea* is, today, 1.5-times greater than that reached by *C. taxifolia* during the period of its maximum expansion. A similar trend has also been observed in France, where the spread of *C. cylindracea* has been described as dynamic and striking at the end of

2007 and where the habitat occupancy increased by 350% in only six years (Cottalorda et al. 2008), as well as in other areas of Italy (Piazzi and Cinelli 1999; Piazzi et al. 2001a) and in Spain (Ruiz et al. 2011), where such an impressive increase was described in only one year. To date, in most of the invaded Mediterranean areas, no reduction in the surfaces colonized has ever been reported (Klein and Verlaque 2008). At present, it is therefore impossible to envisage which of the two models of invasion kinetics (Boudouresque and Verlaque 2012) *C. cylindracea* will follow, i.e. the ‘boom and bust’ previously described for *C. taxifolia* or the most common ‘natural fluctuation model’, which is characterized by a plateau-like persistence phase, despite more or less abrupt fluctuations.

At the beginning of its spread in the Mediterranean Sea, *C. taxifolia* was viewed as a biological pollutant and was defined ‘a major ecological event’ (Boudouresque et al. 1995, 1996). However, the annual spreading rate of 1.63 we computed for its phase of expansion in Liguria was greatly lower than the rate of 6 expected annually by scientists in the early stages of the expansion (Boudouresque et al. 1995). Other studies from the French side of the Ligurian Sea confirmed that, except for the phase of expansion, this alga did not spread as much as previously hypothesised (Jaubert et al. 2003) and showed that this alien was 1 to 2 orders of magnitude less abundant than was commonly believed.

In 2005 at the Gallinara Island (area AG), Tunesi et al. (2007) observed that, notwithstanding its older arrival, *C. taxifolia* reduced its original occupancy and showed less abundant than the more recently arrived *C. cylindracea*. There is no evidence, however, that the latter is actively causing the displacement of the former, although *C. cylindracea* would be favoured with regards to the outcome of the competition over *C. taxifolia* (Piazzi and Ceccherelli 2002). A recent synoptic analysis aimed at evaluating geographical distribution of *C. taxifolia* all around the Mediterranean Sea showed natural regression and disappearance of many stands of this species from the historical sites of occurrence in France, in the Balearic Islands (Spain), in Croatia, in other areas of the South Italy and in Tunisia (Iveša and Devescovi 2006; Langar et al. 2010; Meinesz et al. 2010). The greatest decline of *C. taxifolia* was observed in those areas located in the northernmost sectors of the

Mediterranean Sea, i.e. in the coldest sectors as it is the Ligurian Sea (Bianchi et al. 2013). The large annual variation in the sea temperature has been hypothesised as one of the possible causes of the decline of *C. taxifolia* in the northern and colder sectors of the Mediterranean (Meinesz et al. 2010). Abundance of invasive NIS may strongly fluctuate due to predator-prey relationships, parasite-host relationships, strategies of discontinuous propagule production, unevenness in recruitment, climate episodes, etc. (Boudouresque and Verlaque 2012). A fluctuating growth has already been observed in other species of the genus *Caulerpa*. The native *C. prolifera*, which is also extremely sensible to low temperatures, showed impressive expansion periods in the Mediterranean between 1920 and 1960 (Meinesz 1973), followed by periods of great decline between 1960 and 1980 and, again, another period of expansion between 1980 and 2006. A realistic perspective on the kinetics of the spreading of *C. taxifolia* indicates that the risk posed by this alga to major endemic species is much lower than was formerly predicted (Boudouresque et al. 1995). Today this alga still persists in highly urbanized and disturbed areas, as for instance close to large touristic marinas or sewage systems, or in correspondence of *Posidonia oceanica* dead matte areas, which represent ideal substrata for its spread (Montefalcone et al. 2007b).

Evidence for the resistance of *C. cylindracea* to the low temperatures of the Liguria Sea has been already provided by Raniello et al. (2004) and Cottalorda et al. (2008), likely the reasons of its higher colonization potential than that of *C. taxifolia*. The exclusive aptitude of *C. cylindracea* to adopt three different reproductive modalities (sexual, vegetative by stolonization, and vegetative by fragments) has also been interpreted as another cause of its great expansionistic success (Panayotidis and Žuljević 2001; Renoncourt and Meinesz 2002). Sexual reproduction is likely to assure its continuous spread and prevents any possibility of containment by eradication interventions, which had successfully been done to control the spread of *C. taxifolia* along the French (Cottalorda et al. 2008) and the Italian coasts (in VA and CH areas) in the past. The rapid spread of *C. cylindracea* in the Mediterranean Sea has few equivalents in other introduced marine macrophytes (Verlaque et al. 2004). It was able to colonize virtually all types of substrata in

correspondence of urbanized and polluted areas (Gennaro and Piazzì 2014), as well as of marine protected areas (Katsanevákis et al. 2010; Montefalcone et al. 2010a). Impact of *C. cylindracea* on native ecosystems was significant (Piazzì et al. 2001b; Klein and Verlaque 2008; Piazzì and Balata 2008). Seagrass meadows and coralligenous reefs, which are among the most important coastal habitats in the Mediterranean Sea (UNEP-MAP-RAC/SPA 2008; Pergent et al. 2012), showed a loss of the original structure of their assemblages when invaded by this NIS (Ceccherelli and Campo 2002; Piazzì et al. 2007; Antolić et al. 2008; Baldacconi and Corriero 2009). As many manipulative experiments showed deleterious effects on benthic assemblages following invasion by *C. cylindracea*, its spread at such a wide-spatial scale might have unprecedented impacts on composition and functioning of invaded ecosystems (Strayer 2012), especially considering the burying effects due to its rapid growth and its ability to form multilayered mats during the vegetative season (Piazzì and Cinelli 1999). If the value of 10% is the fraction suggested at which an established invasive NIS affects ecosystem functioning (Strayer 2012), in all the areas of Liguria affected by *C. cylindracea* such a threshold has been exceeded: shall we, thus, translate our future attention and all the concerns posed to the ill-famed ‘killer alga’ *C. taxifolia* to the stronger invader *C. cylindracea*?

The observed differences in the kinetics of spreading experienced by *C. taxifolia* and *C. cylindracea* may be due to differences in the biological characteristics of the two NIS, as well as to different environmental constraints. The Ligurian Sea has very particular climatic conditions that may have favoured expansion of *C. cylindracea* and disadvantaged, in some way, that of *C. taxifolia*, the former being defined as a species with temperate affinities able to withstand cold temperatures (Raniello et al. 2004) whilst the latter with tropical affinities (Meinesz and Hesse 1991). On the contrary, seawater warming and the process of tropicalization of the Mediterranean Sea (Bianchi 2007) were expected to facilitate the spread of *C. taxifolia*. The divergent kinetics of spreading prevents any possibility of generalization of the future behaviour of invasive NIS in the Mediterranean Sea, so that a single model for the spreading of the strong invaders would be not

adequate. In addition, the introduction events of these NIS are generally still too recent to properly assess the phase (expansion or persistence) they are experiencing and therefore the corresponding model ('natural fluctuation' or 'boom and bust'): invasion kinetics is often a long-lasting process and, in most cases, only hypotheses can be drawn (Boudouresque and Verlaque, 2012). The recent EU Directives Marine Strategy Framework Directive and Biodiversity Strategy (EC 2012, 2014) stressed on the importance of the existing NIS datasets for achieving the basic information on their trends in abundance, temporal occurrence and spatial distribution (Galil et al. 2014), although continuous periodic surveys are mandatory to understand the kinetics of their spread and to define specie-specific models. Only from the spatial patterns of NIS spread we will be able to predicate ecological patterns, which are crucial for setting efficient management actions (Galil et al. 2014). However, as *C. cylindracea* received a comparatively lower attention than *C. taxifolia*, no precise estimation on its total habitat occupancy in the Mediterranean Sea is available (Klein and Verlaque 2008). Predicting the effects of invasive NIS on native ecosystems (Strayer 2012) and applying occupancy models (Kéry et al. 2013) to analyse their kinetics require the sustained collection of series of data by targeted long-term studies, chronosequences, repeated mapping and underwater surveys to gather quantitative information.

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## Figure captions and table heading

**Fig. 1** Occurrence and abundance (in ha) of *Caulerpa taxifolia* and *Caulerpa cylindracea* along the Ligurian coastline in the years between 1984 and 2013. See Materials and methods for the code of each coastal area

**Fig. 2** Habitant occupancy (in ha) of *Caulerpa taxifolia* and *Caulerpa cylindracea* in the four periods under investigation, i.e. 1984-1993, 1994-2000, 2000-2008, 2009-2013 (pale grey blocks), with the average trend (thick line) and the annual spread rate ( $r$ ) between periods

**Fig. 3** Change in cover (in %) of *Caulerpa taxifolia* and *Caulerpa cylindracea* in Liguria in the years between 2000 and 2013. Coastal areas where data on cover are not reported correspond to areas where the two NIS had not been observed during scuba surveys, or where their occurrence was under the detectable threshold. See Materials and methods for the code of each coastal area

**Table 1** Results of 2-way ANOVAs on the % cover of *Caulerpa taxifolia* and *Caulerpa cylindracea*. See Materials and methods for the code of the coastal area

Table 1

Source of variation	df	<i>Caulerpa taxifolia</i>			<i>Caulerpa cylindracea</i>		
		MS	F	p	MS	F	p
Period (P)	1	19.35	5.41	0.036	70.88	7.48	0.016
Area (A)	14	14.13	286.92	0.000	43.06	22.81	0.000
A × P	14	3.58	72.65	0.000 <sup>a</sup>	9.48	5.02	0.000 <sup>b</sup>
Residual	150	0.05			1.89		
Cochran's C-test		C = 0.34, p < 0.01			C = 0.13, p < 0.05		
Transformation		Ln (x+1)			Sqrt (x+1)		

<sup>a</sup> A × P:

MO, VM, OS, SR, AG: 2000-2008 > 2009-2013

<sup>b</sup> A × P:

MO, VM, OS, SR, AG, PO, FR, MM: 2000-2008 < 2009-2013

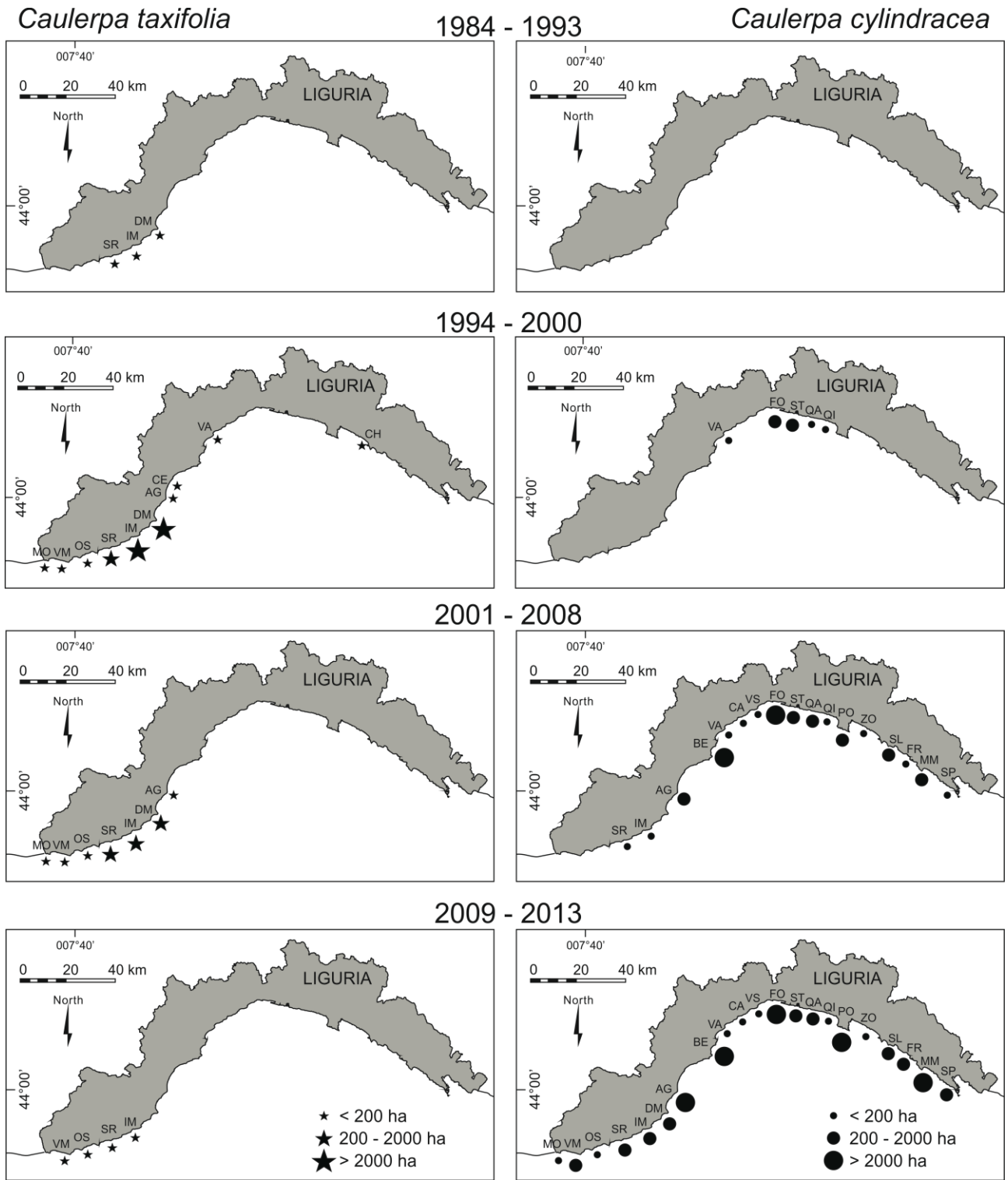


Figure 1

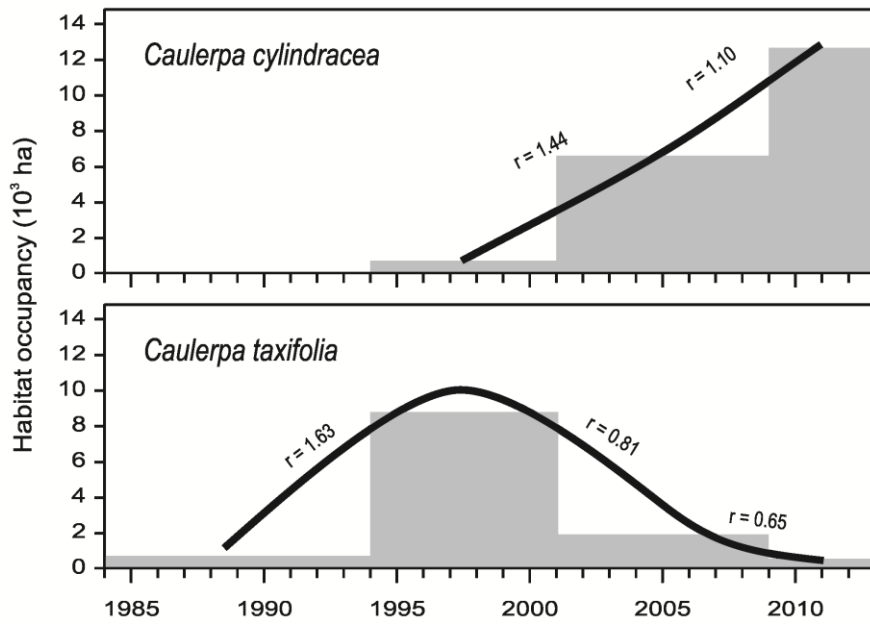


Figure 2

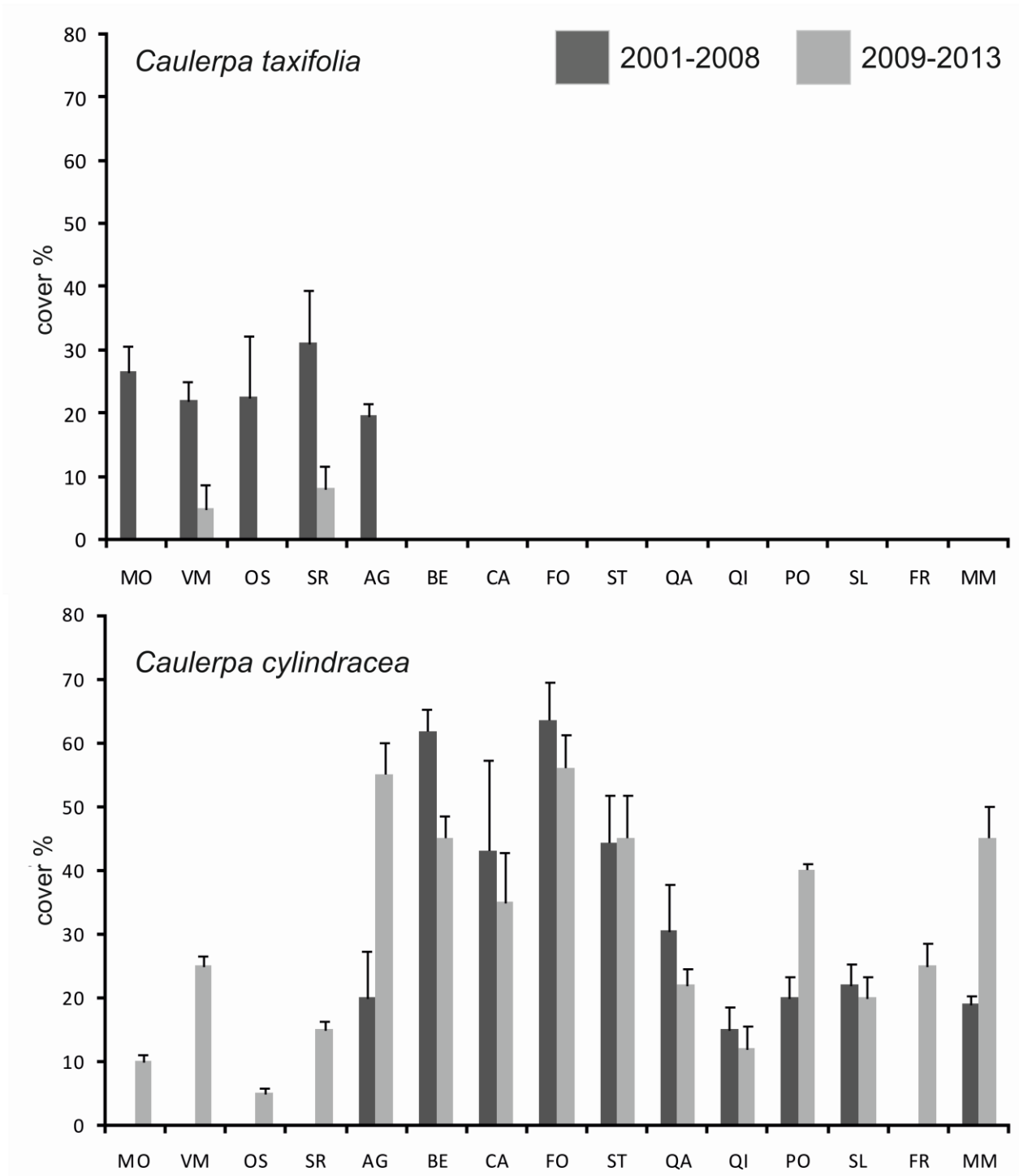


Figure 3