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Ester Cecere, Giorgio Alabiso, Roberto Carlucci, Antonella Petrocelli* and Marc Verlaque

Fate of two invasive or potentially invasive alien seaweeds in a central Mediterranean transitional water system: failure and success

Abstract: Over the past 15 years, populations of two invasive or potentially invasive alien seaweeds have been studied by means of both quantitative and qualitative methods in the Mar Piccolo basin in Taranto (Southern Italy, Mediterranean Sea). The dynamics of the cold-temperate brown seaweed *Undaria pinnatifida* (Alariaceae, Laminariales) showed a boom-and-bust path, ending in apparent local extinction. In contrast, the tropical red seaweed *Hypnea cornuta* (Cystocloniaceae, Gigartinales) has shown a steadily invasive path since its introduction. The respective failure and success of these marine alien species were analysed in relation to their biological and ecological traits and the environmental characteristics of the Mar Piccolo in comparison with other Mediterranean coastal lagoons. The study confirms that temperature and salinity monitoring in the recipient region could provide a first estimation of the invasive potential of an alien species soon after its introduction.

Keywords: alien species; *Hypnea cornuta*; Mediterranean Sea; transitional water systems (TWS); *Undaria pinnatifida*.

Introduction

Human activities are responsible for species introduction, which is one of the major aspects of globalisation, and the increase in international maritime trade has considerably

facilitated this phenomenon (Galil et al. 2007, Hewitt et al. 2007, Perrings et al. 2010). Alien species are considered as a major threat to marine biodiversity (Katsanevakis et al. 2014). Moreover, owing to their capacity to alter ecosystem composition and processes (Olenin et al. 2007, Suárez Jiménez et al. 2015) as well as the negative consequences of carrying parasites and pathogens (Diamant et al. 2007, Perrings et al. 2010), their economic impact should not be underestimated (Katsanevakis et al. 2014).

With about 1000 alien species recorded, excluding microalgae, the Mediterranean Sea is one of the geographical areas most severely affected by this phenomenon (Zenetos et al. 2012). Soon the situation could become significantly worse due to the recent enlargement of the Suez Canal (Galil et al. 2015), which is considered one of the main vectors of introduction of alien species (Galil 2009, Zenetos et al. 2010). However, aquaculture also has a considerable responsibility as a vector of introduction. Starting in the 1970s, there were massive importations of spat and adults of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) for aquaculture purposes in the Mediterranean, mainly from Japan (but also from British Columbia and Korea), without any effective system of decontamination and quarantining (Boudouresque et al. 2011). Since this date, many species originating from cold to temperate regions of the North Pacific Ocean have been introduced (Verlaque et al. 2007, Zenetos et al. 2010). With regard to the seaweeds, those introductions mainly occurred in transitional water systems (TWS), where aquaculture activities are commonly carried out, such as Thau Lagoon, France (Boudouresque et al. 2011), the Venice Lagoon, Northern Adriatic Sea (Marchini et al. 2015) and the Mar Piccolo of Taranto, Northern Ionian Sea (Cecere et al. 2016a). These sites represent three hotspots of species introduction in the Mediterranean, and are therefore continuously monitored for early detection of any new introduction.

Notwithstanding the impact of species introductions, few methods are as yet available to assess the fate of an introduced species and the risk of invasion (Roy et al. 2014), or to manage and control the development of their populations after introduction (Simberloff 2009, Ojaveer et al. 2014). For this purpose, the study of the dynamics of alien species once introduced is of great interest, especially

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Wallentinus 2005). A good knowledge of the ecology and life history traits of alien species (eco-physiology, reproductive pattern, growth rate, vulnerability to diseases, predation and competition) can offer a basis for identifying the threshold values of environmental triggers of biological invasions (Knoepffler-Péguy et al. 1985, Meinesz et al. 2001, Gollasch 2002, Sagerman et al. 2014). This knowledge can be useful to anticipate the outcome of a potentially invasive alien species in the short, medium or long term, providing a basis for the choice of suitable management procedures in order to minimise its impact on the ecosystems and on human activities (Meinesz 2007, Rilov and Galil 2009, James et al. 2015).

Today, there is a serious concern about global warming, and there is ongoing and lively debate in the scientific community about its putative role in facilitating the success of species introductions (Boudouresque and Verlaque 2010). Recently, an extensive study carried out in the Ligurian Sea showed that, in this cold sector of the Mediterranean, the spread of alien seaweeds seems to be mostly due to their “large native geographical ranges” rather than to a considerable increase in local seawater temperatures (Parravicini et al. 2015a). However, some authors consider that the success of an alien species might depend on both its native range, which could be cold, temperate, tropical or cosmopolitan, and the environmental features of the recipient area (mainly temperature) (Boudouresque and Verlaque 2010 and references therein, James et al. 2015). In this respect, global warming might affect the success of alien species more at a local scale than at a wider scale, causing local peaks of variation in sheltered, shallow and enclosed environments, such as TWS, which are exposed to wider ranges of temperature

variation than the open ocean. In the Mediterranean, this might be the case for coastal lagoons such as the Mar Piccolo of Taranto, where a slight trend of temperature increase was recently recorded (G. Alabiso, unpublished data). The aim of this study was to carry out a multi-year monitoring survey of populations of two potentially invasive alien species introduced in the Mar Piccolo of Taranto, and having contrasting native ranges: the Japanese cold-temperate brown seaweed *Undaria pinnatifida* (Harvey) Suringar, found for the first time in the Mediterranean Sea in 1971 (Thau Lagoon; Anonymous 1980), and the pantropical red seaweed *Hypnea cornuta* (Kützinger) J. Agardh, found for the first time in the Mediterranean in 1894 (Rhodes Island; Reinbold 1898), although incorrectly identified as *H. valentiae* (Turner) Montagne.

We focused on salinity and seawater temperature, mainly with regard to annual variation and extreme values, as factors that could have affected the fate of both alien species, even though all the environmental variables, and their synergistic effect, are recognised as important (Dukes and Mooney 1999, Báez et al. 2010, Cook et al. 2013).

Materials and methods

Study site

The Mar Piccolo of Taranto is a coastal nearly enclosed basin located to the north of the town of Taranto. Its surface area is ca. 20 km² and it is divided by two promontories of land into two smaller basins, which are called the First and the Second Inlets (Figure 1). The maximum depths in the central part of the First and Second Inlet are

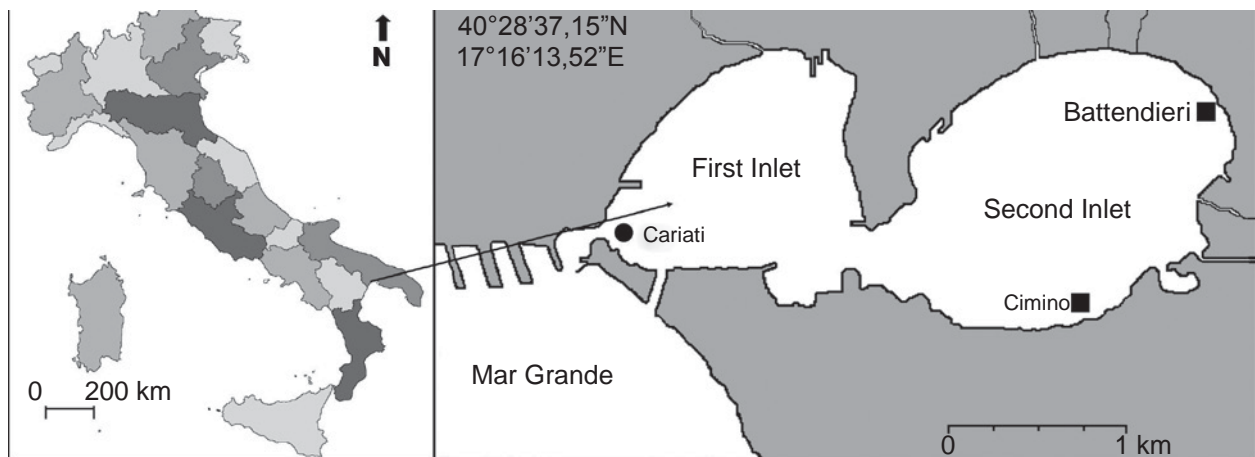


Figure 1: Map of Mar Grande and Mar Piccolo of Taranto with sampling stations for each species.

◆: *Undaria pinnatifida*, Cariati (First Inlet); ■: *Hypnea cornuta*, Battendieri and Cimino (Second Inlet); left, location of Taranto in Italy.

12 and 8 m, respectively. Most of the hard substrata are artificial. The soft substrata are sandy near the shore and muddy in the central zones. Cecere and Petrocelli (2009) present a detailed description of the site with the variations of the main physico-chemical variables, and highlight the presence of several possible activities and vectors favouring the introduction of alien seaweeds (e.g. mussel importation, military ships, fishing boats). To date, a total of 35 non-indigenous marine species (15 macroalgae, 8 protists and 12 invertebrate metazoans) have been found in the Mar Piccolo (E. Cecere, unpublished results). Some of these, presumably introduced by shipping, were observed in the 1920s, giving rise to transitory populations (Pierpaoli 1923), but most have been detected since the late 1980s, and many of them were probably associated with shellfish importations.

Alien species

Undaria pinnatifida (Alariaceae, Laminariales, Phaeophyceae) has an annual heteromorphic diplohaplontic life history, with the alternation of a macroscopic sporophyte generation and a microscopic dioecious gametophyte generation. Sporophytes have a short stipe and a blade with shallow pinnate divisions. Reproduction occurs when the size of individuals exceeds 20 cm in height. Unilocular meiosporangia with paraphyses are produced on two opposite jabot-shaped wings (sporophylls) arranged along the stipe (Castric-Fey et al. 1993, NIMPIS 2016 and references therein). The survey of the introduced population was initiated at Cariati in 1998. Monthly quantitative sampling was carried out during the growth period of sporophytes in 2000–2001, 2001–2002 and 2006–2007. This monitoring survey lasted up to May 2015 but, since sporophytes became more difficult to find, quantitative sampling was not possible after 2007. Each month, 30 quadrats (50 × 50 cm) were haphazardly sampled by SCUBA diving. The total number of sporophytes and their distribution per size class on the basis of the total length (TL in cm) were determined in each quadrat. The density of the population was expressed as the mean number of sporophytes per m² (No m⁻²) and the recruitment was estimated as the number of young sporophytes (TL < 10 cm) per m².

Hypnea cornuta (Cystocloniaceae, Gigartinales, Florideophyceae) is a species characterised by the presence of stellate branchlets that act as vegetative propagules (Yamagishi et al. 2003, Cecere et al. 2004). Like all the species of the genus, it has a *Polysiphonia*-type life history with the alternation of an isomorphic diploid tetrasporophyte and haploid dioecious gametophytes, with a

diploid carposporophyte developing on the female gametophyte (Masuda et al. 1997).

A monitoring survey of introduced populations was initiated in December 2000 at Battendieri and in October 2007 at Cimino (Figure 1). Monthly quantitative sampling was carried out from 2007 to 2010, and in 2014 and 2015 at both Battendieri and Cimino. Each time, three quadrats (50 × 50 cm) were sampled at 1-m depth and the collected thalli were preserved in 5% formalin-seawater. For each quadrat, the blotted fresh weight of *H. cornuta* was measured on a triple beam balance. The biomass of *H. cornuta* was expressed as the mean fresh weight per m² (g fw m⁻²).

Seawater temperature

The seawater temperature (in °C) was continuously recorded at 1-m depth in the sampling stations by means of an underwater probe (IDROPROBE Idromar, Genoa, Italy) from 1996 to 2004, and by temperature loggers S2T (NKE Instrumentation, Hennebont, France) from 2005 to 2015. The mean annual values were calculated as well as the mean temperatures of the coldest and warmest weeks of each year, which were considered a proxy of minimum and maximum mean values.

Statistical analysis

In order to analyse the occurrence of significant changes by season in the density and recruitment of *Undaria pinnatifida* and biomass of *Hypnea cornuta* during the investigated period, parametric analysis of variance (ANOVA) was performed using the SPSS version 17.0 (Chicago, IL, USA) (SPSS Inc. 2009). Seawater temperature data were analysed by non-parametric regression.

Results

Undaria pinnatifida

In April 1998, sporophytes of *Undaria pinnatifida* were found for the first time in the First Inlet of the Mar Piccolo of Taranto attached to the mooring wharf of the small local fishing fleet, close to the numerous shellfish shops at Cariati in the old town of Taranto (Figure 1; Cecere et al. 2000). In 1998 and 1999, sporophytes were restricted to the wharf at Cariati, and ropes and pebbles lying on the nearby muddy bottom, from the sea surface to 1.5-m

depth. Later, some sporophytes were also present on the floating pontoons facing the wharf. The longest specimen observed was about 1-m long and the individuals exhibited great morphological variability. Examination of the sporangial sori showed complete maturation of the sporangia. The density and the size structure of sporophytes varied widely through the year (Figures 2 and 3). New sporophytes were detected from December to April, with a peak in February 2002. They grew up to late spring (May–June) and disappeared completely in summer (July). In May, the smallest sporophytes (i.e. 0–10 cm) consisted entirely of residual stipes of old specimens (Figures 2 and 3). The largest individuals were observed from March to May (Figure 3). The densities observed in winter 2002 were much higher than those recorded in 2001. In 2003 and 2004, *U. pinnatifida* stopped spreading in the basin. In 2005 and 2006, a slight reduction in the population was observed. In 2007, the first new sporophytes were detected later (in February) and, during this year, the mean density of sporophytes never exceeded two individuals m^{-2} (Figure 3). Very few sporophytes (total < 10) were observed in 2008 and 2009 and none since 2010. The inter-annual differences in the density of sporophytes were statistically significant ($p < 0.05$).

Hypnea cornuta

Since 2000, *Hypnea cornuta* has spread constantly in the Second Inlet of the Mar Piccolo. In December 2000, *H. cornuta* was found for the first time at Battendieri (Figure 1; Cecere et al. 2004). Afterwards, in 2007, it

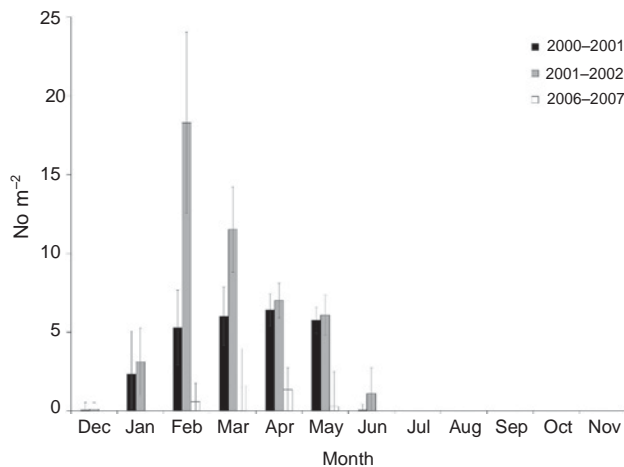


Figure 2: *Undaria pinnatifida*: density of recruits (No. m^{-2}) in 2000–2001, 2001–2002 and 2006–2007 at Cariati (First Inlet). Data are means \pm SD ($n = 60$).

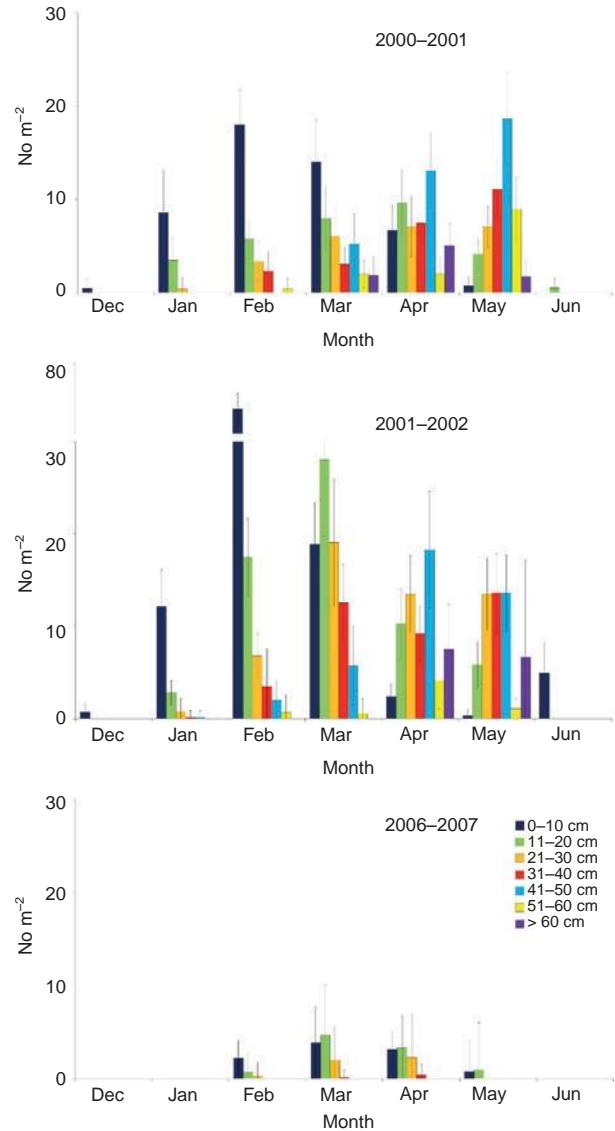


Figure 3: *Undaria pinnatifida*: densities of sporophytes in different length classes, expressed as means (\pm SD) of data from 30 quadrats in 2000–2001, 2001–2002 and 2006–2007 at Cariati (First Inlet). Sporophytes were absent in quadrats from July to November.

was found at Cimino (Figure 1), where imported mussel packaging is performed. The vegetative multiplication of the alga occurs through the production of stellate propagules and modified unattached pigmented fragments of thallus that act as over-wintering organs up to the next spring (Cecere et al. 2004). In December 2008, fertile tetrasporophytes were observed for the first time, whereas fertile gametophytes were never found. At Battendieri and Cimino, the biomass of *H. cornuta* was maximal during summer and negligible during winter and early spring. The quantitative survey showed that the biomass of *H. cornuta* increased regularly each year from 2007 to

2015, and was significantly higher at Battendieri than at Cimino (Figure 4). The highest biomasses were measured in August 2015 at both stations (5860 and 3477 g fw m⁻² at Battendieri and Cimino, respectively; Figure 4). Seasonal variations of biomass were statistically significant ($p < 0.05$) among years and between stations.

Seawater temperature

For the study period (1996–2015), in the Mar Piccolo, the annual range of seawater temperature was wide (about 15–24°C). The minimum and maximum mean temperatures of the coldest and warmest weeks were registered in January 2002 ($7.51 \pm 0.85^\circ\text{C}$) and June 2003 ($32.29 \pm 0.93^\circ\text{C}$), respectively. An increasing trend of ca. 1°C was observed in the mean annual temperature from 1996 to 2015 ($p < 0.01$), but no significant trend was observed in the mean values of coldest and warmest weeks of each year (Figure 5).

Discussion

A biological invasion, which involves many interacting factors (physiological traits of the potential invader, size

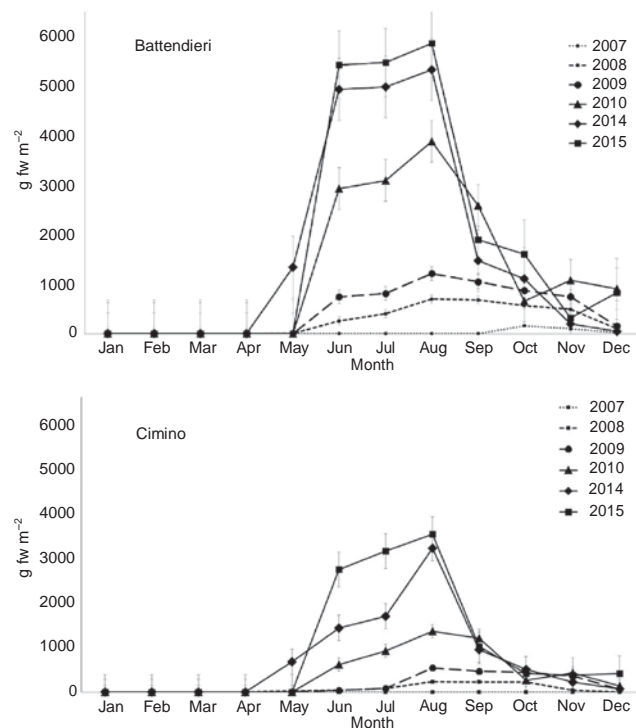


Figure 4: *Hypnea cornuta*: biomass (g fw m⁻²) from 2007 to 2010, and in 2014 and 2015 at Battendieri and Cimino (Second Inlet). Data are means \pm SD ($n = 3$).

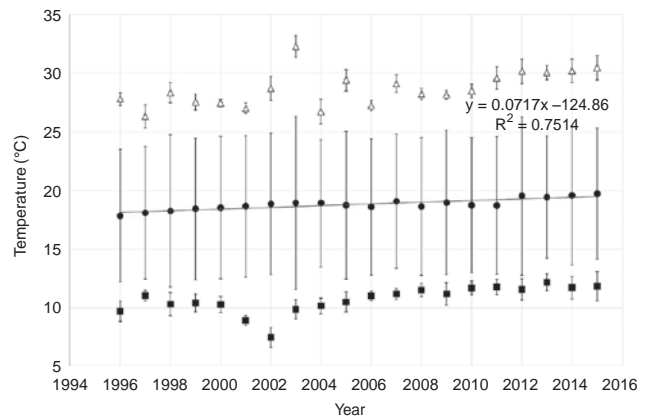


Figure 5: Annual mean temperatures (\blacklozenge) and mean temperatures of coldest (\blacksquare) and warmest (\triangle) weeks from 1996 to 2015 in the Mar Piccolo. Data are means \pm SD ($n = 8736$).

and number of inoculum and characteristics of donor and recipient ecosystems), can be broken down into three phases: arrival, establishment and ecological integration (Vermeij 1996, Valentine et al. 2007, Boudouresque and Verlaque 2012). The last phase can require several years or decades, so long-term monitoring is essential. Unfortunately, the arrival of a species at a new locality attracts more attention than its absence from a previously occupied site (Boudouresque and Verlaque 2010), so long-term studies such as the present one are less frequent than first reports (Klein and Verlaque 2012). In the same way, even though the introduction of a potential invasive species does not always foreshadow establishment and invasion (Simberloff and Gibbons 2004, Walther et al. 2009), less is known about introductions that fail.

In the Mar Piccolo of Taranto, the dynamics of two potential invaders were monitored, on the basis of both quantitative and qualitative observations. Two different demographic paths were identified: the first (*Undaria pinnatifida*) corresponds to the boom-and-bust model, which occurs when the alien species reaches a peak of development before declining, sometimes to local extinction (Williamson 1996); the invasive path of the second species (*Hypnea cornuta*) corresponds to the natural fluctuation model characterised by a plateau-like persistence phase with fluctuations (see Boudouresque and Verlaque 2012).

Undaria pinnatifida is a cold-temperate species described from Honshu (Japan) and widely cultivated in the NW Pacific Ocean (China, Japan and Korea), and on the NE Atlantic Coast, where it has been deliberately introduced in France (Pérez et al. 1992, Floc'h et al. 1996). As an alien species, it occurs in all the continents, except Africa and Antarctica (Wallentinus 2007) and it is considered as one of the “World’s 100” and “Mediterranean’s

100 Worst Invasive Alien Species” (Streftaris and Zenetos 2006, GISD 2016). In the Mediterranean Sea, it has been reported only from the north-western basin (France, mainly in Thau Lagoon), the North Adriatic Sea (Venice Lagoon, Italy) and the Mar Piccolo of Taranto. One year after its discovery in the Mar Piccolo, the mean density of *U. pinnatifida* sporophytes (18 individuals m⁻²) was higher than that recorded in the Venice Lagoon (about 10 individuals m⁻²; Curiel et al. 2001) and lower than that in the Thau Lagoon (250 individuals m⁻²; Boudouresque et al. 1985). The first detection of new sporophytes was later in the Mar Piccolo of Taranto than in the two other coastal lagoons (December–February vs. November), and both a shortening of the recruitment period and a lowering of its intensity were observed throughout the study period, although the growth of sporophytes went as far as complete sporangial maturation. Although *U. pinnatifida* is flourishing in the Thau Lagoon and the Venice Lagoon (Verlaque 2001 and unpublished data, Sfriso and Facca 2013), the species quickly declined in Mar Piccolo to apparent collapse 12 years after its first sighting.

In terms of disturbance and turbidity, these three large TWS are similar, whereas salinity and temperature are usually higher in the Mar Piccolo (Table 1). As far as water temperature is concerned, optima for the growth of the sporophyte and the gametophyte of *U. pinnatifida* are 3.5–20°C and 10–24°C (Sanderson 1990), while the upper lethal temperatures are >22–25°C and >30°C, respectively (Table 1).

In Brittany, under optimal seawater temperatures, sporophyte recruitment started at the end of autumn and extended to late spring (Castric-Fey et al. 1999). In regions where temperatures do not exceed 19°C, sporophytes persist all the year; elsewhere they disappear in summer and early autumn when only microscopic gametophytes are present (Akiyama and Kurogi 1982, Stuart et al. 1999). Observations in the Japanese native area showed that, at 28°C, less than 15% of gametophytes survive and the extinction of *U. pinnatifida* is forecast if local temperature rises (Watanabe et al. 2014).

As a result, the winter-spring temperature ranges of the Mar Piccolo of Taranto allowed growth and reproduction of sporophytes. The “weak point” of the life cycle of *U. pinnatifida* concerns the sexual generation: summer seawater temperatures in the Mar Piccolo were frequently higher than the lethal temperature range, probably inducing high mortality and failure of reproduction of gametophytes, leading to the collapse of the population. Other environmental factors, in combination with temperature, may have also contributed to the failure of the naturalisation of *U. pinnatifida*. Firstly, there is the salinity of the Mar Piccolo that was close to or higher than the lethal threshold both for gametophytes and sporophytes (Table 1). Similarly, too high a salinity (37–38; Hopkins 1985) along the north-western Mediterranean coasts might explain the failure of the naturalisation of *U. pinnatifida* in open sea, while the species is flourishing in the less salty waters of the Thau Lagoon (Boudouresque et al. 1985, Knoepffler et al. 1990, Verlaque et al. 2015). Overgrazing by the sea-urchin *Paracentrotus lividus* (Lamarck, 1816), already observed in Thau Lagoon (M. Verlaque, unpublished data), could hardly have occurred in the Mar Piccolo because the sea urchin density never exceeded 1–2 individuals m⁻² (E. Cecere and A. Petrocelli, unpublished data). Metal contamination could have also played a negative role. Experiments showed strong inhibition of both meiospore germination and gametophyte development by copper (Leal et al. 2016), a metal strongly present in the superficial sediments of the Mar Piccolo, especially in the First Inlet (Petronio et al. 2012).

Hypnea cornuta is a warm-water species mentioned as widespread in tropical and sub-tropical zones, although the worldwide distribution of *Hypnea* species must be considered with caution because of multiple confusion with identification (Mshigeni and Chapman 1994). In the Mediterranean Sea, where the species is considered as an alien seaweed from the Red Sea (Verlaque et al. 2015), it was reported from the eastern Mediterranean basin (Greece, The Middle East and Egypt), the Mar Piccolo of Taranto and, more recently, north-eastern Sicily (Manghisi

Table 1: Salinity and seawater temperature ranges in the Thau Lagoon, the Lagoon of Venice and the Mar Piccolo of Taranto, and salinity and temperature tolerances for the sporophytic and gametophytic generations of *Undaria pinnatifida*.

	Salinity	Temperature	References
Thau Lagoon	27–40	(4–) 5–27 (–29)°C	Jouffre and Amanieu 1991, Plus et al. 2003
Lagoon of Venice	(20–) 27–34 (–35.9)	(–1) 5–26 (–33)°C	Curiel et al. 2001, Sfriso et al. 2009, Sfriso and Facca 2013
Mar Piccolo of Taranto – First Inlet	33.04–37.81	7.5–32.29°C	Cecere and Petrocelli 2009
Lethal values for gametophytes	< 15 and > 34	< –1°C and > 30°C	Saito 1975, Bardach et al. 1982, Sanderson 1990, Pérez et al. 1992, O’Loughlin et al. 2006, Peteiro and Sánchez 2012
Lethal values for sporophytes	< 15 and > 34	< 0°C and > 22–25°C	

et al. 2011), Tunisia (Sghaier et al. 2016) and the Tyrrhenian Sea (Cecere et al. 2016b). With regard to the TWS of the north-western Mediterranean basin (Thau) and the Northern Adriatic Sea (Venice), we note the absence of this tropical species. In the Red Sea, the temperature and salinity ranges are 18–32°C and 36.5–40.5, respectively (Edwards 1987). In Israel, experimental cultures of *H. cornuta* have succeeded with temperature and salinity ranges of 14.5–30.5°C and 30–36, respectively (Friedlander and Lipkin 1982), which are close to values recorded in the Mar Piccolo, at least in summer for temperature. Monthly observations carried out in the Mar Piccolo highlighted a seasonal cycle of development, with a growth period from May to August and a resting period from January to April, during which the species was only represented by over-wintering organs (basal parts, stellate propagules and pigmented unattached fragments; Cecere et al. 2004, 2011). Fertile gametophytes were never observed, suggesting that the rare tetrasporangia are apomeiotic or that they fail to germinate. Multi-year monitoring confirmed the invasive behaviour of the species, with a steady increase in biomass throughout the study period. Although *H. cornuta* became the dominant component of the summer free-living seaweed assemblages, no conspicuous noxious effects on benthic assemblages or human activities have so far been detected. In Israel and Brazil, experiments on *H. cornuta* showed a positive correlation between seawater temperature and growth rate, with the fastest growth (up to a doubling of initial weight, i.e. 100 g in Israel, after 3 days cultivation), when seawater temperature reached the highest values (about 30°C) (Friedlander and Zelikovitch 1984, Yokoya and Oliveira 1992). Therefore, high seawater temperature could explain the success of *H. cornuta* in the Mar Piccolo of Taranto. Frequently close to 30°C in summer, temperature was most probably responsible for the invasive path of the species. The analysis of temperature trends shows yearly fluctuations, with on-going warming observed since 2002, which might have contributed to the steady increase of biomass. In addition to the role played by high temperatures, the high rate of vegetative multiplication of *H. cornuta* (pigmented fragments, propagules and possible apomeiotic sporangia) might also have favoured its establishment in the Mar Piccolo, as already observed in the case of some other marine and terrestrial introductions (Nyberg and Wallentinus 2005, Walther et al. 2009).

The comparison of the dynamics of *U. pinnatifida* and *H. cornuta* in the Mar Piccolo of Taranto showed that salinity and temperature could be important environmental variables affecting the fate of introduced species. The Mar Piccolo seems to be too salty and too warm for

U. pinnatifida, and not too cold and favourable for *H. cornuta*. In Norway, the alien seaweed *Heterosiphonia japonica*, which is able to survive between 1°C and 28°C, did not spread along the coasts, where seawater temperatures normally go down to 0°C (Bjærke and Rueness 2004). The invasive strain of *Caulerpa taxifolia* failed to settle in Japanese seawaters because of temperatures lower than 10°C (Komatsu et al. 2003). In the Mar Piccolo of Taranto, this might be also the case for the highly invasive cold-temperate species *Codium fragile* var. *fragile*. It was found for the first time in the basin in 2000, and was not observed again until 2009 when a new introduction occurred (Petrocelli et al. 2013); nowadays, it survives with only a few scattered individuals at the site of the second introduction (Petrocelli et al. 2013).

Once the ecological requirements, and especially the lethal limits, of an alien species are known, the continuous recording of salinity and seawater temperature in the introduction zone, to determine not only the trends but also their fluctuations throughout the year, could offer a highly informative basis for predicting the fate of alien species at a local scale (Dukes and Mooney 1999, James et al. 2015). However, it would be advisable to consider also the shift from the theoretical niche (based upon e.g. temperature and salinity) towards the actual, realised niche, taking into account biotic interactions within the ecosystem, which is still undervalued in marine ecosystems (Parravicini et al. 2015b).

It is well known that maximum and minimum temperature values can be more important than annual mean values in affecting the population dynamics of a species (Stachowicz et al. 2002, James et al. 2015). Such values will be all the more extreme where water bodies are restricted and shallow, like the TWS.

While an increase in temperature of 1°C–1.4°C over the last 30 years was reported for the Mediterranean Sea (see Lejeusne et al. 2010 and references therein), a similar warming of mean annual temperature (ca. 1°C) was recorded in the Mar Piccolo of Taranto since 1996 (G. Alabiso, unpublished data). Moreover, during the last decade, some anomalous peaks of temperature have been recorded throughout the Mediterranean Sea (Lejeusne et al. 2010). Such climatic events can induce dramatic changes in the latitudinal distribution and development of native and alien species. In the Mar Piccolo, the extreme values for the water surface temperature seem to have played a more crucial role with regard to the fate of species invasion than the recent warming trend observed.

In the future, a warmer Mediterranean Sea should be more welcoming for tropical than for cold-temperate alien species, and make easier their establishment, spread

and eventually, invasiveness (Occhipinti-Ambrogi and Galil 2010). Simultaneously, cold-temperate alien species should be disadvantaged (Boudouresque and Verlaque 2010). Thus the Mar Piccolo of Taranto could become more unfavourable for cold-temperate alien species such as *U. pinnatifida* and more welcoming for tropical species such as *H. cornuta*, all the more so as it is located on the westward spread route of Red Sea species coming into the Mediterranean Sea via the Suez Canal.

Among the alien marine macrophytes of the Mar Piccolo, only the tropical *H. cornuta* has displayed an invasive trend, but without any apparent noxious effects. However, an alien species can spend a transitional period of several years before giving rise to a successful invasion (Simberloff and Gibbons 2004 and references therein, Walther et al. 2009). For instance, the red seaweed *Gracilaria salicornia* became invasive almost 30 years after its intentional introduction into Hawaii (Smith et al. 2004). Therefore, the continuous monitoring of *H. cornuta* in the Mar Piccolo of Taranto is strongly recommended. Furthermore, occasional very low seawater temperatures could cause the transitory spreading of cold-temperate aliens that could damage the recipient ecosystem as well, before undergoing a definitive collapse (Simberloff and Gibbons 2004). Therefore, the monitoring of these alien species is also advisable.

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Roberto Carlucci is Assistant Professor in Ecology. His main research interest is focused on the application of biological, statistical and mathematical models to marine ecology and population dynamics. In particular, his research is oriented to provide scientific advice to regional, national and EU administrations for the setting of the best practice in the Mediterranean for a sustainable exploitation of marine resources. He uses the statistical and geostatistical packages (SPSS, Statistica, PRIMER V, ISATIS – Geovariance) and ARCVIEW GIS. He has (co)-authored more than 70 scientific publications in congress proceedings, national and international ISI journals. RC is a reviewer for international ISI journals.



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Antonella Petrocelli is a researcher at the Phycology Laboratory. Her research activity deals with marine biology, phycology and ecology with regard to: biodiversity; habitat destruction; bioremediation; biotechnologies; ecophysiology; alien seaweeds; cultivation in little

and meso scale of marine macroalgae; floristic and vegetational studies in marine benthic communities; biology of seaweeds with particular reference to vegetative propagation; active metabolites from marine macroalgae; ecophysiology of seaweeds with particular reference to photosynthesis; seagrasses.



Marc Verlaque

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Marc Verlaque is a retired researcher who continues his research activities in the GIS Posidonie, a non-profit organization hosted by the Mediterranean Institute of Oceanography (Aix-Marseille University). His study fields deal with marine macrophytes (algae and sea grasses), biology of conservation and species invasions, marine ecology, taxonomy, biogeography and phylogeny.