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Research Article

Rapid expansion and potential range of the invasive kelp *Undaria pinnatifida* in the Southwest Atlantic

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Abstract

Coastal Patagonia, often regarded as a pristine area of the world, has been invaded by non-indigenous species that are rapidly modifying local ecosystems. One of the most conspicuous invaders is the kelp *Undaria pinnatifida*. First recorded near the city of Puerto Madryn (Argentina, 42.75°S) in 1992, *Undaria's* range has expanded more than five degrees of latitude to the south during the last 15 years. By 2007 it was first detected north of Valdés Peninsula (a natural barrier to dispersal), beginning its northward expansion, and between 2007 and 2011 spread along the coasts of San José and San Matías gulfs at an average rate of ~50 km yr^{-1}. A small population was detected in Mar del Plata (Argentina, 38.04°S) in 2011, more than three degrees of latitude to the north, suggesting a new human-mediated inoculation. A thermal tolerance window is hypothesized based on experimental information and remotely sensed sea-surface temperature (SST) at the latitudinal range limits of *U. pinnatifida* populations worldwide. The window is defined by average SSTs ranging between -0.6 °C and 16.8 °C in the coldest month, and between 13°C and 28°C in the warmest month. Using climatologic satellite SST from several locations, a potential latitudinal thermal range extending between Puerto Deseado (Argentina, 47.75°S) and Cape Torres (Brazil; 29.35°S) is predicted. Salinity and substrate quality however constrain suitable habitat in the Southwest Atlantic to discrete stretches of coastline, suggesting that the northern potential boundary would be around La Coronilla (33.90°S), on the Uruguayan coast.

Key words: seaweed, exotic, sea-surface temperature, wakame, Patagonia, geographic range

Introduction

Coastal Patagonia has often been perceived as a pristine area; however, this area has been invaded by many non-indigenous species, which are rapidly modifying local ecosystems (Orensanz et al. 2002). One of the most conspicuous invaders is *Undaria pinnatifida* (Harvey) Suringar (Laminariales, Ochrophyta) (hereafter referred as *Undaria*), a brown macroalga native to eastern Asia (Saito 1975). During the last forty years, this species has successfully invaded many coastal areas around the world (Wallentinus 2007). Invasiveness is related to its ability to rapidly colonize artificial substrates and disturbed areas, fast growth, tolerance to adverse conditions, and the ability of nearly invisible gametophytes to form "seed banks" (Hewitt et al. 2005; Wallentinus 2007).

Undaria was first recorded in the Southwest Atlantic coastal waters in 1992, near the city of Puerto Madryn, Argentina (PM; Nuevo Gulf; Figure 1) (Casas and Piriz 1996). The alga spread along the coast at a rate of about 1 to 5 km yr^{-1} (Piriz and Casas 2001). By late 1999, it was found near the city of Camarones (Figure 1), about 250 km south from PM (Orensanz et al. 2002), and in the spring of 2005 was recorded 300 km farther south, near the city of Puerto Deseado (Martín and Cuevas 2006). During the 15 years that followed the introduction of *Undaria* in PM, the extensive spread of the species (more than five degrees of latitude) proceeded only southwards, suggesting that the Valdés Peninsula (Figure 1) functioned as a natural barrier to northward dispersion. However, early in 2007, *Undaria* was first recorded in the San

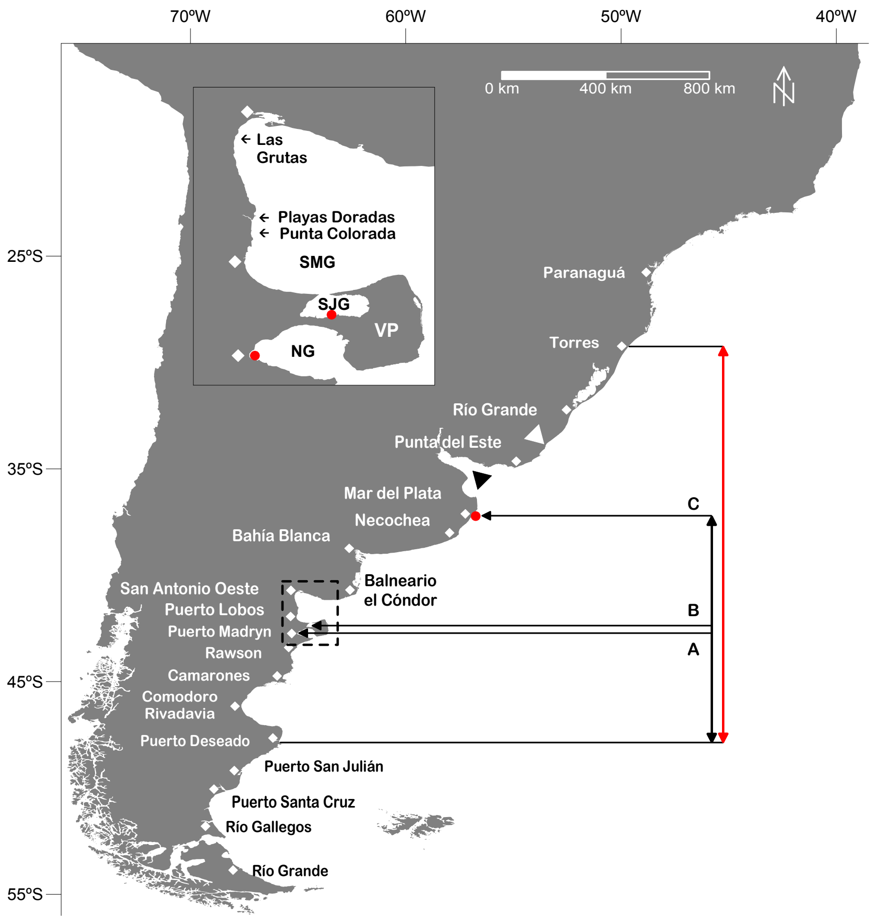

Figure 1. Coastal locations along the Southwest Atlantic. The black and red vertical arrows indicate the actual and the potential range, respectively, of *Undaria* distribution based on thermal tolerance. Horizontal black lines indicate the predicted northern and southern range limits. Horizontal arrows and red dots indicate locations of human-mediated inoculation of *Undaria* (A: Puerto Madryn, 1992; B: Punta Tehuelche, 2007; C: Mar del Plata, 2011). Triangles indicate political limits between Argentina and Uruguay (black, Río de la Plata estuary) and between Uruguay and Brazil (white). Inset: northern Patagonian gulfs: San Matías (SMG), San José (SJG) and Nuevo (NG); Valdés Peninsula (VP) and resorts in SMG where *Undaria* is present (Punta Colorada), and where it has not been yet observed (Playas Doradas and Las Grutas).

José Gulf (SJG; Figure 1) (Ramón Rosales pers. comm.), north of the peninsula. An artisanal fisherman reported seeing the alga on the south margin of the Gulf, close to Punta Tehuelche, a popular recreational fishing destination. The San José Gulf is part of the Valdés Peninsula Protected Area, a natural reserve designated by UNESCO as a World Heritage Site because of its significance for marine conservation. The Gulf is physically connected with the larger San Matías Gulf (SMG); a complex circulation system governs water exchange between the two basins (Amoroso and Gagliardini 2010; Amoroso et al. 2011). The presence of *Undaria* in this ecologically sensitive area made likely its spread to the north, raising public concern for several reasons. Research tracking the invasion in Patagonia showed that, because of its large size (up to 2 m in length; Raffo et al. (2009)) and invasive characteristics (Wallentinus 2007), dense kelp beds can outcompete native macroalgal species (Casas et al. 2004; Torres et al. 2004), while positively affecting diversity and abundance of benthic macrofauna (Irigoyen et al. 2011b). Also, *Undaria* produces a negative visual impact and induces changes in fish behavior in near-shore reefs used for recreational diving (Irigoyen et al. 2011a). Finally, large volumes of algal biomass get stranded on sandy beaches near Puerto Madryn (Eyras and Sar 2003; Piriz et al. 2003), affecting the attractiveness of the beach for recreational users. *Undaria* represents more than 50% of the algal biomass stranded during the summers (Eyras and Sar 2003; Piriz et al. 2003), the tourist season. Regular clean-up efforts require a significant expenditure for the municipal authority.

In 2008, the Ministry of the Environment of the Chubut Province (Argentina) implemented regulations intended to control the spread of *Undaria* in SJG. Regulatory measures involved the manual removal of macroscopic sporophytes and a regular monitoring program to track and eventually prevent its dispersal. Despite control efforts, the invasion of *Undaria* is progressing: its presence has been recently reported in Mar del Plata Harbor, more than 1000 km north from PM (Meretta et al. 2012). While this puts pressure on the Argentine Environmental Ministry to define a national management strategy, studies of the invasion of *Undaria* in other regions of the world suggest that its eradication is not feasible once populations are well established (New Zealand Ministry of Fisheries 2001; Forrest 2007; Commonwealth of Australia 2008). It might be possible, however, to prevent or control the undesired invasion of aquaculture facilities, recreational destinations, or marine protected areas; i.e., "post-border management" (Forrest 2007; Forrest et al. 2009). Knowledge of the likelihood of the species getting established in potentially receptive areas, and the delimitation of possible "internal borders" (natural barriers for natural dispersal within the potential geographic range) could be key pieces of information to define management measures like vector control across internal borders or monitoring programs for early-detection (Forrest et al. 2009).

In this study, information was collated on the fine-scale geographical distribution of *Undaria* in the most recently invaded areas, SJG and the adjacent SMG, by combining all the available information (systematic sampling, removal efforts and opportunistic sampling on beaches). Based on sea-surface temperature (SST) data, the potential of *Undaria* to further extend its geographic range along the coasts of the Southwest Atlantic was examined. Finally, the availability of suitable coastal habitats relative to salinity and substrate was evaluated as a constraint on the spread of *Undaria* within its potential thermal range in the Southwest Atlantic.

Materials and methods

Distribution of Undaria *in the northern Patagonian gulfs*

The distribution of *Undaria* along the coasts of SJG and SMG (Figure 1) was recorded, combining diving sampling along random and fixed transects with searches for beached sporophytes. Every year since 2001, between January and March, a diving survey has been conducted in SJG to assess scallop stock biomass prior to the fishing season (Ciocco et al. 2006). Surveys are conducted along fixed transects perpendicular to the shoreline (1–25 m depth); each transect is divided into 100-meter segments. Starting in March, 2008, after fishermen alerted authorities about the presence of *Undaria* in SJG, divers conducting the scallop survey were instructed to record the presence of living plants in each segment along the transects. This protocol was followed in surveys conducted in 2008, 2010 and 2011. Additionally, from February 2008 through December 2010, the provincial environmental authority conducted a monitoring program involving monthly diving surveys on random transects placed along the coasts of SJG. In a less systematic way, occurrence of *Undaria* was monitored between January and May 2011 at the southwestern and northwestern coasts of SMG. Following incidental reports, diving surveys were conducted along random transects and beached sporophytes were searched for concurrently.

Surveyed locations and *Undaria* records were mapped for every annual life-history cycle between June 2007 and May 2011. The annual cycle was defined as spanning the period between June of year i and May of year i+1, considering that the sporophyte (visible) phase of *Undaria's* life cycle starts growing in July-August and vanishes in March-April (Casas et al. 2008; Irigoyen 2010). Given the uneven distribution of sampled locations in space and time, the total range of occupied coastline was determined at the beginning and end of the study period, and was the basis for estimating average range expansion rate.

Potential geographic range of Undaria *along the coasts of the southwestern Atlantic*

Following Floc'h et al. (1991), SST was used to assess the maximum potential latitudinal range of *Undaria* along the coasts of the Southwest Atlantic. A literature review, complemented with expert consultation, was conducted to determine the northern and southern distribution limits of

Table 1. Northern and southern distribution limits of *Undaria pinnatifida* in native and invaded regions, and average SST during the warmest and coldest month at each location

Region	Distribution limits	Lat	Lon	Warmest SST (ºC)	Coldest. SST (ºC)	Source
Native range						
Japan	North	45.42	141.46	20.0	2.0	Saito (1975)
“”	South	31.85	130.15	28.0	16.8	Saito (1975)
Russia	North	43.04	132.11	20.2	-0.6	Skriptsova et al. (2004)
China	South	30.72	122.80	27.3	9.3	Yamanaka and Akiyama (1993)
Invaded regions						
Europe (Atlantic)	North	51.90	3.91	19.0	5.5	Wallentinus (2007)
“”	South	40.64	-8.75	18.8	13.8	Araujo et al. (2009)
Europe (Mediterranean)	North	45.40	12.43	25.9	8.4	Wallentinus (2007)
“”	South	40.43	17.11	26.1	13.5	Cecere et al. (2000)
North America (Pacific)	North	37.83	-122.42	14.8	11.0	Zabin et al. (2009)
“”	South	31.77	-116.87	20.3	14.8	Aguilar-Rosas et al.(2004)
Australia (mainland)	North	-37.87	144.94	20.1	11.2	Primo et al. (2010)
“”	South	-38.75	143.68	18.0	13.5	Primo et al. (2010)
Tasmania	North	-41.26	148.36	18.0	12.6	Crawford (2007)
“”	South	-43.17	147.55	16.8	11.3	Bryant (2011)
New Zealand	North	-36.42	174.81	20.9	14.4	Russell et al. (2008)
“”	South	-48.03	166.54	13.3	10.7	Nelson (2013)
Argentina	North	-38.03	-57.52	20.3	10.5	Meretta et al. (2012)
“”	South	-47.75	-65.92	13.0	6.0	Martin and Cuevas (2006)

Undaria over its current geographic distribution, including its native range (Japan, Korea, Russia and China) as well as areas where the species has become established and naturalized (Europe, North America, New Zealand, Australia, and Tasmania) (Table 1). To evaluate the potential range of *Undaria* in the Southwest Atlantic, 19 coastal locations spread along 30 degrees of latitude (25°S to 55°S) were selected (Figure 1). Locations were selected to include those close to harbors or marinas, which could facilitate the establishment of *Undaria*.

Ten years (1996–2005) of SST data obtained by the Advanced Very High-Resolution Radiometer (AVHRR) on board of NOAA satellites, processed by the Pathfinder Project (http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/) and available from http://podaac-tools.jpl.nasa.gov/las were used to characterize relevant aspects of the thermal regime at [i] the north and south limits of distribution of *Undaria* in its native range and in regions where it has been introduced (Table 1), and [ii] the 19 selected locations along the coasts of the Southwest Atlantic (Figure 1). The data consisted of monthly composite images with a resolution of ~9 km. SST data were retrieved from the land-free grid cell (0.25° × 0.25°, approximately 9 pixels) closest to each location of interest. Average and standard deviation of the climatologic SST (years pooled) were calculated for each month of the year and used as a proxy of near-shore monthly average SST at a decadal time scale. Climatologic SST based on AVHRR has been widely used to characterize thermal regimes in the Southwest Atlantic (Rivas 2010). Correlation with field measurements has proved satisfactory even in coastal environments, as shown by Williams et al. (2010) for the sector of SMG where *Undaria* has expanded its range in recent years. It must be stressed that the scale of these results is intentionally constrained by SST averaging. Patterns at a spatial scale smaller than ~20 km of coastline and year-to-year variability are beyond the scope of this study.

Average monthly SST for the warmest and coldest months at the limits of native and introduced areas of distribution were used to define the thermal tolerance window suitable for the species to establish sustained populations. Reported thermal constraints for growth and reproduction were gathered from published experimental studies in order to provide ancillary criteria. Summer and winter SST at coastal locations of the Southwest Atlantic (Figure 1) were compared with the

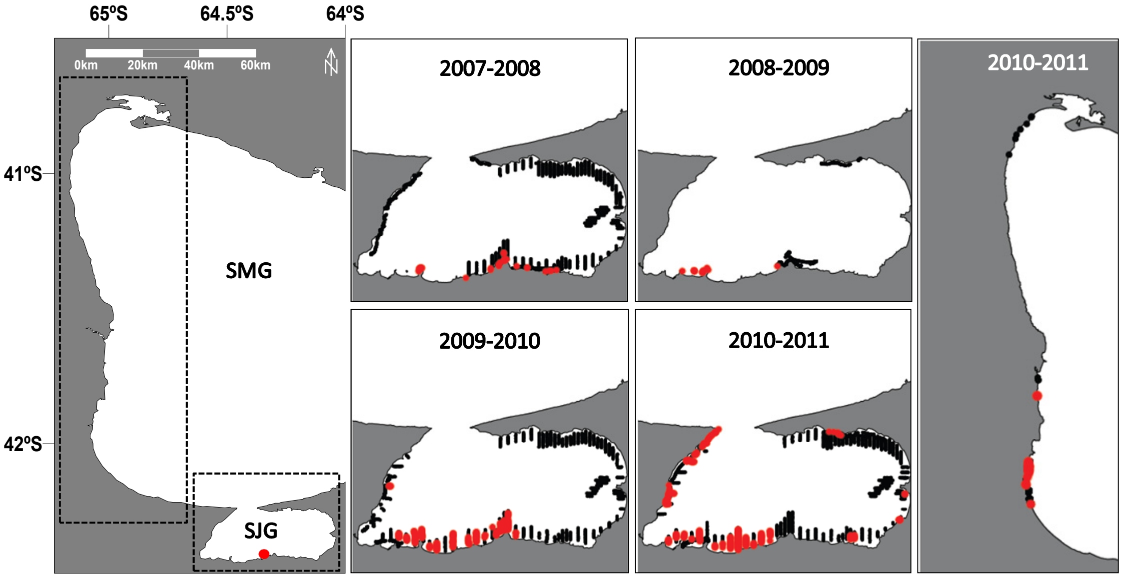

Figure 2. *Undaria* distribution in the northern Patagonian gulfs during four annual cycles, May 2007 to April 2011. Left panel: The San Matías (SMG) and San José (SJG) gulfs; red dot: location of the first *Undaria* record in SJG (Punta Tehuelche). The other panels illustrate surveyed locations (black dots) and *Undaria* records (red dots) along the coasts of SJG (four central panels), and SMG (panel on the right) for each annual cycle.

estimated thermal tolerance window in order to predict the potential of *Undaria* to establish beyond the boundaries of its present range.

Suitable habitat consists of natural rocky shores and human constructions. The distribution of natural rocky shore habitat (including friable sedimentary rocks) was assessed with the geological charts of Dirección Nacional de Minería y Geología del Uruguay (DINAMIGE 2009) (scale 1:500,000) and Secretaría de Geología y Minería de la Argentina (SEGEMAR 2000a, b) (scales 1:250,000 and 1:2,500,00), supplemented when necessary with satellite imagery available from Argentina's Comisión Nacional de Actividades Aero-Espaciales (CONAE) through the Centro Nacional Patagónico (CENPAT, Argentina).

Results

Expansion of Undaria *in the northern Patagonian gulfs*

Monitoring after the first reports of *Undaria* in SJG (2007) indicated that its range had spread considerably (Figure 2). While in 2007–2008 and 2008–2009, it was recorded only along the south coast of the gulf, subsequent surveys (2009–2010 and 2010–2011) showed an expansion to the east, northeast, and west coasts (Figure 2). While records from the first two annual surveys showed *Undaria* present only in the shallow subtidal zone, by the end of the study the occupied depth had expanded to the entire range covered by the survey (5–25 m; Figure 2). In SMG, *Undaria* has been detected only along the southwest coastline. The northernmost record was from near Punta Colorada (41.69°S), where beached sporophytes were found near an iron ore shipping facility. Given lack of monitoring before 2010, it is not possible to assess the exact time of arrival to that area. Between the first survey for SJG in early 2008 (Figure 2) and March 2011, *Undaria*'s range expanded 156 km to the west/northwest, reaching the southwest of SMG (Figure 2). This expansion occurred during three seasonal cycles and represented a dispersal rate of about 50 km yr^{-1}.

Potential geographic distribution of Undaria *in the Southwest Atlantict*

The native range of *Undaria* extends from northwestern Hokkaido to southwestern Kyushu in Japan (Saito 1975; Table 1), and from Peter the Great Bay in Russia (Skriptsova et al. 2004) to the Hangzhou Bay in China (Yamanaka and Akiyama 1993). Within that range, wild populations of *Undaria* live in environments with average monthly SST ranging between -0.6°C and 16.8°C

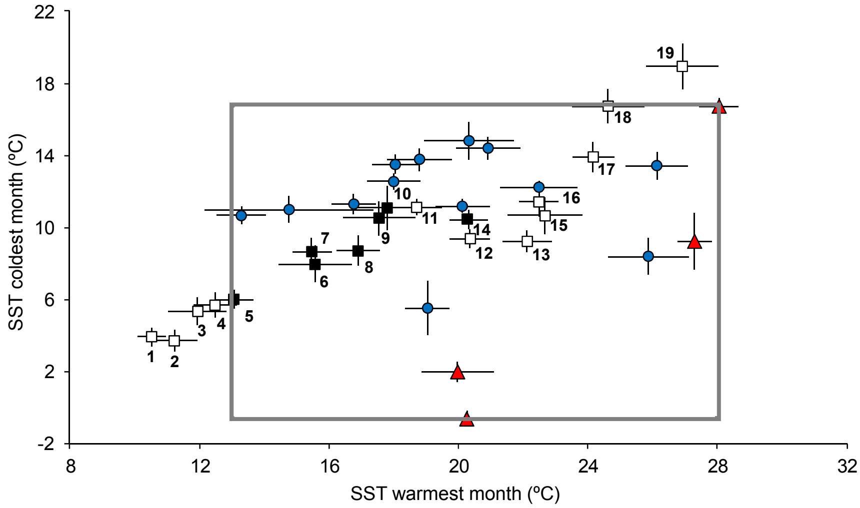

Figure 3. Monthly-averaged (period 1996–2005) sea surface temperature (SST) during the coldest and warmest month of the year at different locations. The red triangles and blue circles represent the geographical limits of native and exotic distribution (with the exception of the southwestern Atlantic coast) of *Undaria*, respectively (see Table 1). Squares correspond to locations where *Undaria* has (filled) or has not (empty) been recorded along the coasts of the southwestern Atlantic; locations numbered in order from south (1: Puerto Deseado) to north (19: Paranaguá) as shown in Figure 1. Vertical and horizontal lines: standard deviations. Grey contour: inferred thermal window for *Undaria* establishment.

in the coldest month, and between 20°C and 28°C in the warmest month (Table 1). At the southern and northern ends of invaded regions the coldest monthly SST ranges between 5.5°C and 14.8°C, and the warmest between 13.0°C and 26.1°C (Table 1). The SST range of the coldest month in invaded regions does not exceed that of the native region; however, the lower SST during the warmest month is 7°C colder than in the native region (Table 1). Based on these results, the thermal window at which *Undaria* could survive was considered to be constrained to between -0.6°C to 16.8°C for the coldest month and between 13°C and 28°C for the warmest month (Figure 3). Accordingly, the potential range of distribution of *Undaria* in Southwest Atlantic coastal waters extends from Puerto Deseado (Argentina, 47.75°S) to Torres (Brazil, 29.35°S) (Figures 1, 3). On the Argentine coast, *Undaria* is actually distributed from Puerto Deseado to Punta Colorada (41.69°S; Figure 1), and was recently found in the Mar del Plata Harbour (38.04°S; Figure 1). The warmest monthly average SST at Puerto Deseado corresponds to the lowest recorded at the high-latitude endpoints of *Undaria's* world range (Figure 3, Table 1). It is highly

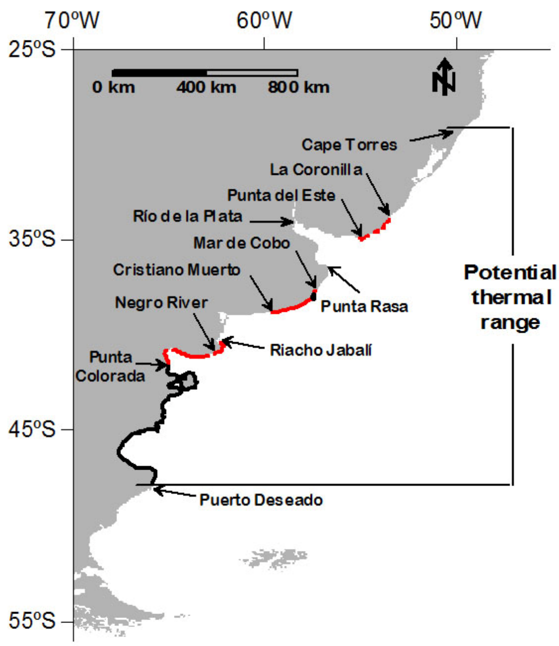

Figure 4. Southwest Atlantic coast with indication of sectors of interest (see Table 2 for description). Black: present *Undaria* distribution; red: sectors where thermal regime, substrate and salinity are suitable for *Undaria* establishment.

Table 1. Coastal sectors of the Southwest Atlantic, within the predicted thermal range for *Undaria*, that are suitable or unsuitable (shaded) for the establishment of *Undaria* with regards to salinity and substrate availability. Sectors (0-7) numbered from south to north (see Fig. 4).

Sector	Range and boundaries	Type of substrate and salinity	References
0	Puerto Deseado (47.75°S) to Punta Colorada (41.69°S)	Range already invaded by *Undaria*. A variety of rocky shores, including friable sedimentary rocks, and coastal stretches with volcanic rocks of Jurasic age or Paleozoic granites.	SEGEMAR (2000a) (charts 4166-IV, 4363-I, 4566-II, 4566-III and 4766-III)
1	Punta Colorada to Riacho Jabalí (40.59°S)	West coast of SMG: mixture of hard sedimentary rocks of Siluric age, Paleocene calcareous sedimentary rocks and Ordovicic granites; north and northeast coasts of the sector: abrasion platforms of Quaternary friable sedimentary rock, ending near the mouth of the Negro River.	Olivier (1973); Escofet et al. (1978); SEGEMAR (2000a) (chart 4166-II)
2	San Blas (40.20°S), Anegada and Blanca bays, east to Cristiano Muerto (39.00°S)	A succession of shallow bays, salt marshes, mud flats and exposed sandy beaches, generally unsuitable habitat for *Undaria* except for a few man-made structures in the area of Bahía Blanca	Escapa et al. (2004); Isacch et al. (2006); Olivier and Penchaszadeh (1968); SEGEMAR (2000b)
3	Cristiano Muerto to Mar de Cobo (37.77°S)	Mostly abrasion platforms of cineritic friable sedimentary rocks of Quaternary age (clay-silt or clay, continental deposits of aeolic or lacustrine origin). The only exception is a very short stretch of very hard marine sedimentites of Ordovicic age (Balcarce Formation) located at Mar del Plata, where *Undaria* has been recorded.	López Gappa et al. (1990);Adami et al. (2004); Adami et al. (2008); Olivier et al. (1966); Vallarino (2002); SEGEMAR (2000b)
4	Mar de Cobo to Punta Rasa (36.32ºS)	Estuarine salt marshes (Mar Chiquita Lagoon) and extensive exposed sandy beaches. No suitable habitat for *Undaria*.	Olivier et al. (1972); Olivier and Penchaszadeh (1968); SEGEMAR (2000b)
5	Punta Rasa to Punta del Este (34.95°S)	Mouth of La Plata River estuary, a major barrier to the potential northern dispersal of *Undaria*	
6	Punta del Este to La Coronilla (33.90°S)	Extended sandy beaches punctuated by rocky headlands, composed mostly of Cambric and pre-Cambric granitoids or volcanic-sedimentary sequences.	Maytía and Scarabino (1979); Borthagaray and Carranza (2007); DINAMIGE (2009)
7	La Coronilla to Cape Torres (29.35°S)	Extensive exposed sandy beaches (approximately 680 km), interrupted only by a few estuarine environments, minor with the exception of the mouth of the Los Patos Lagoon (32.16º S). Only hard substrates are a few man-made structures, including the docks at the entrance of the lagoon. Major barrier to the spread of *Undaria*	Gimenez and Yanicelli (2000); Gianuca (1983);
	Cape Torres	Isolated rocky outcrop; SST at the upper end of potential thermal tolerance range of *Undaria*. Invasion considered unlikely.	

unlikely that the species could survive in locations to the south, because of cold summers (Figure 3). On the other hand, SST in Mar del Plata ranges from 10.4°C to 20.3°C, well within the estimated window of thermal tolerance. Cape Torres (Brazil; 29.35°S), where SST ranges from 16.8°C to 24.6°C, corresponds to the northern predicted limit for its distribution in the south-western Atlantic (Figure 1); the species would not be able to cope with warmer winters at locations to the north (Santa Catarina State). While the species may have reached its potential southern limit of distribution in the Southwest Atlantic, it could still spread farther north.

Within its potential latitudinal range, as defined by thermal boundaries, the spread of *Undaria* in the Southwest Atlantic is constrained by the availability of suitable substrate. Natural rocky shores (including friable sedimentary rock) consist of stretches separated by significant ecological barriers (Figure 4; Table 2 and references therein). Major barriers are: [1] the coasts extending from north of the mouth of the Negro River to Cristiano Muerto, which includes the extensive salt marshes and mud flats of the San Blas, Anegada, and Blanca bays, as well as long stretches of exposed sandy beach; [2] extensive exposed sandy beaches north of Mar de Cobo (north of Mar del Plata), combined with the La Plata River estuary; and [3] extensive exposed sandy beaches (ca. 680 km) between La Coronilla (Uruguay) and Cape Torres (Brazil). The latter, an isolated rocky outcrop, corresponds (as mentioned earlier) to the upper potential limit of thermal tolerance for *Undaria*.

Discussion

In a risk assessment conducted by Nyberg and Wallentinus (2005), *Undaria pinnatifida* was ranked the third most hazardous of 113 macroalgal species introduced to Europe. During the last forty years, it has invaded many temperate coasts around the world (Wallentinus 2007; Dellatorre et al. 2012). In the Southwest Atlantic, dispersal proceeded at a slow pace following initial introduction to Nuevo Gulf; range expanded about 20 km after 8 years (Piriz and Casas 2001; Orensanz et al. 2002). Natural dispersal occurs during the sporophytic phase by means of both spores and drifting detached sporophytes (Russell et al. 2008). Estimated spore-mediated dispersal rate is in the order of 1–100 m yr^{-1} (Brown 1999), while sporophyte drift can increase the dispersal rate to 1–10 km yr^{-1} (Sliwa et al. 2006). While the relatively slow expansion previously reported within Nuevo Gulf (Piriz and Casas 2001; Orensanz et al. 2002) is consistent with natural dispersion, it has been speculated that shipping (or some other human activity) mediated *Undaria*'s spread beyond the Gulf's boundaries. Its range has expanded more than five degrees of latitude to the south during the last 15 years (Martin and Cuevas 2006), and by 2007 it was first detected north of Valdés Peninsula (a natural barrier to dispersal), beginning its northward expansion. Once the invasion passed the Valdés Peninsula barrier, northwards dispersal seems to have accelerated. If natural dispersal were assumed, the rate of spread along the coasts of SJG and SMG observed in this study is one of the fastest and most comprehensively documented for the species (Piriz and Casas 2001; Cremades Ugarte et al. 2006; Forrest 2007; Russell et al. 2008). Different mechanisms may have contributed to accelerate dispersal of *Undaria* in our study region. Intense tidal currents and complex circulation patterns are known to facilitate the advection of objects adrift (Amoroso and Gagliardini 2010), and detached sporophytes would not be an exception. However, artisanal and recreational fishing boats operating in SMG and SJG were likely contributing vectors.

Established populations, from Puerto Deseado to Punta Colorada, have the potential for further spread via natural mechanisms (e.g. spores and drifting sporophytes) and human activities. The recent report of a wild population in Mar del Plata (Meretta et al 2012) can be considered as evidence of the latter, because movement from Punta Colorada (previous northern limit) to Mar del Plata could not be achieved by means of natural dispersal mechanisms alone (Brown 1999; Sliwa et al. 2006). Across relatively large spatial scales (e.g. tens of kilometers or larger), *Undaria's* natural dispersal is likely to be prevented by barriers in the form of extensive tracts of deep water, severe wave-exposure or soft sediments (Sinner et al. 2000). The latter, in the form of extensive mud flats and exposed sandy beaches, predominate north of Bahía Blanca (Table 2).

Many abiotic factors, including salinity, light, nutrients, wave exposure, and substrate availability, are known to influence environmental suitability for *Undaria* (Saito 1975; Floc'h et al. 1991; Wallentinus 2007). However, water temperature is recognized as the most important environmental variable affecting the ecology of the species (Saito 1975) and its reproduction (Saito 1975; Morita et al. 2003a, b), thus being the primary factor governing the potential boundaries of its geographic range. Based on estimated SST, the potential distribution of *Undaria* in the Southwest Atlantic spans more than 18 latitudinal degrees. This is wider than the latitudinal range in its native area (approximately 15 degrees of latitude). A lower amplitude of seasonal temperature fluctuations in the Southwest Atlantic could partly explain the difference. Minimum and maximum average monthly SST at the boundaries of *Undaria*'s geographic distribution world-wide (-0.6°C and 28.0°C), are consistent with reported thermal tolerances for growth and survival (Saito 1975; Henkel and Hofmann 2008). Reproductive activity appears to be further constrained by two thermal thresholds: average temperature has to be above 13°C–14°C during the warmest month for sporulation (Saito 1975; Thornber et al. 2004), and below 20°C during the coldest month for sexual development and maturation of the gametophytes (Saito 1975; Morita et al. 2003a; Thornber et al. 2004; Henkel and Hofmann 2008).

Given the nature of the observations presented here and, consistent with it, the spatial and temporal resolution of averaged SST data, the relation between SST and *Undaria*'s distribution pattern at small spatial scales (less than ~20 km of coastline) or over the short-term are beyond the scope of this study. On the other hand, our results provide a baseline for assessing future change in the geographic range of *Undaria*, whether as a result of ongoing dispersal or of long-term climate change (Jueterbock et al. 2013). Year-to-year SST variability at the studied coastal locations in the Southwest Atlantic coast (Figure 3, SDs between 0.5°C and 1.2°C) could lead to the formation of transient populations of *Undaria* outside the predicted range (Duarte et al. 2013). Extralimital records and transient populations have been reported for a number of organisms in the region (Orensanz et al. 2002), particularly in the form of transient populations of subtropical species south of the La Plata River estuary.

The potential for spread of *Undaria* north and south of its present range in the southwestern Atlantic is asymmetrical. The species has already reached the southern limit of its predicted distribution at Puerto Deseado (47.75°S). While average SST for the coldest month at that location (~6°C) is well above the low threshold for *Undaria* survival, average SST during the warmest month (~13°C) is much lower than that recorded at the northern limit of its native range (~20°C), and approximately on the lower threshold for sporulation (Saito 1975; Thornber et al. 2004). Supporting predictions, eight years after having been recorded for the first time in Puerto Deseado, *Undaria* is not known to have spread southwards despite recent careful inspection of rocky shores in the region of San Julian, the next township to the south (J.P. Martin, pers. comm.). It is considered highly unlikely that *Undaria* could invade the southern tip of continental South America, the Magellan Strait and Tierra del Fuego. However, were *Undaria* introduced by human activities to the Southeast Pacific, specifically the Chilean coast north of the Magellanic region, it could potentially thrive over a geographic range even more extensive than along the Atlantic coast (Carrasco and Barón 2010).

North of the Mar del Plata area, where it was recently reported, natural dispersion of *Undaria* is unlikely given the presence of a major barrier formed by extensive exposed sandy beaches, salt marshes on the south coast of the La Plata River estuary, and the estuary itself (Acha et al. 2008). Eventual introduction to the Uruguayan coast would require human-mediated activities. Along the north coast of the estuary, salinities below 27, necessary for sporophytic growth (Saito 1975), would constrain westward penetration. Rocky outcrops along the Atlantic coast of Uruguay are, however, vulnerable in terms of substrate suitability, salinity, and thermal regime. Expansion beyond the area of La Coronilla (Uruguay) and along the coasts of southern Brazil (State of Rio Grande do Sul) is unlikely, as the 680 km coastline consists almost exclusively of exposed sandy beaches, a phenomenal barrier. Monthly average SST at Cape Torres (29.35°S, Brazil), an isolated rocky outcrop that corresponds to the northern end of the potential thermal range of *Undaria* in the southwestern Atlantic, ranges from 16.8 to 24.6°C. While the upper monthly SST is well within *Undaria's* tolerance, the lower monthly mean SST is similar to that reported at the southern limit in Japan (Table 1). Morita et al. (2003a) reported a sharp decrease of gametophytic maturation rate between 15°C (~90%) and 20°C (~10%); it is not likely that winter SST over 16.8°C would favor sexual development of the gametophyte. Yet, some authors have reported sexual maturation of *Undaria* gametophytes at temperatures up to 20°C (Saito 1975; Thornber et al. 2004; Henkel and Hofmann 2008). Thus, the northern limit prediction should be considered conservative; northern locations might be colonized only if gametophytes could reproduce within the range 17°C–20°C. Cape Torres, geographically isolated and marginally suitable because of thermal regime, is unlikely to be colonized by *Undaria*, leaving the La Coronilla area as the most likely northern limit for its potential spread in the Southwest Atlantic.

Significant stretches of the Southwest Atlantic coast are still at risk of invasion. Vector control and surveillance are needed to prevent inoculation into new areas (Hulme et al. 2008), particularly the Atlantic coast of Uruguay. Implementation of those measures requires knowledge of the realized and potential range of the species in the region, and identification of natural barriers for natural dispersal within "internal borders" (Forrest et al. 2009). Both aspects were investigated as part of this study. The results presented here should assist in the design and timely implementation of monitoring and prevention programs.

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