The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina)

Graciela Casas[1],*, Ricardo Scrosati[2] & María Luz Piriz[1]

[1]*Centro Nacional Patagónico (CONICET), Boulevard Brown s/n, 9120, Puerto Madryn, Chubut, Argentina;* [2]*Department of Botany, University of British Columbia, Vancouver, Canada;*
*Author for correspondence (e-mail: graciela@cenpat.edu.ar; fax: +54-2965-451543)

Abstract

The kelp *Undaria pinnatifida* (Phaeophyceae) is a seaweed native to northeast Asia, but during the last two decades, it has been accidentally or intentionally introduced in several temperate coasts worldwide. In central Patagonia (Argentina), this species was first detected in late 1992, and it is progressively spreading from the point of introduction. Through a manipulative experiment involving *Undaria* removal in 2001, we found that its presence is associated with a dramatic decrease in species richness and diversity of native seaweeds in Nuevo Gulf. Future prospects are worrisome, as, in addition to the negative impact from a biodiversity viewpoint, native commercial macroalgae and invertebrates might also be affected.

Introduction

The introduction of marine exotic species may result in severe ecological perturbations in native communities (e.g. Bax et al. 2001; Piriz and Casas 2001; Grosholz 2002). In seaweed assemblages, competition for light and substrate can be intense, leading to the local exclusion or sharp decrease of native species (DeWreede 1996). Exotic species that spread beyond the point of introduction and become regionally abundant are termed invasive species (Richardson et al. 2000, Kolar and Lodge 2001). Seaweed invasions may result from intentional or accidental introductions, and they have been reported worldwide. Well-known examples are *Undaria pinnatifida* (Harvey) Suringar and *Sargassum muticum* (Yendo) Fensholt, among the brown algae, and *Codium fragile tomentosoides* (van Goor) Silva and *Caulerpa taxifolia* (Vahl) C. Agardh, among the green algae (Walker and Kendrick 1998). Due to the magnitude of its ecological impact,

the *C. taxifolia* case has received particular attention from researchers (e.g. Boudouresque et al. 1995; Bellan-Santini et al. 1996; Verlaque 1996; Ceccherelli and Cinelli 1999; Smith and Walters 1999; Ceccherelli and Piazzi 2001).

Undaria pinnatifida is a kelp species (Phaeophyceae, Laminariales) native to northeast Asia (Akiyama and Kurogi 1982), but it has successfully invaded several areas of the world, such as France, England, Holland, Belgium, western United States, New Zealand, Australia, and Argentina (Pérez et al. 1981; Hay and Luckens 1987; Sanderson 1990; Floc'h et al. 1991; Piriz and Casas 1994; Fletcher and Manfredi 1995; Campbell and Burridge 1998; Dumoulin and De Blauwe 1999; Stegenga 1999; Silva et al. 2002).

In December 1992, *Undaria pinnatifida* (hereafter referred to as *Undaria*) was detected close to the international dock of Puerto Madryn, central Patagonia, Argentina. Likely vectors of introduction were the ballast water or fouling of cargo ships or fishing vessels from Japan or Korea

(Piriz and Casas 1994). Since that initial sighting, basic research has been performed on its reproductive phenology and geographic expansion in this area (Casas and Piriz 1996). An essential part of impact assessment is to determine the effects of an invasive species on the local biota. This paper reports changes in species richness, diversity, and evenness of native seaweed assemblages from central Patagonia associated with the *Undaria* invasion. We predicted a lower number and diversity of native seaweeds in the presence of *Undaria*.

Materials and methods

The study site was a rocky subtidal area at about 6 m depth, relative to the mean tidal level, near Cuevas Point, in Nuevo Gulf, Patagonia, Argentina (42°46.80′ S, 64°59.46′ W, Figure 1). At this site, the algal assemblage invaded by *Undaria* was previously characterized by the dominant presence of *Codium vermilara* and crustose Corallinaceae, in addition to other small algal species. The sea surface temperature ranges annually between monthly means of 8.7 and 18 °C (Casas and Piriz 1996). The effects of *Undaria* on richness, diversity, and evenness of local seaweed assemblages were determined by a manipulative experiment of *Undaria* abundance.

In April 2001, all *Undaria* thalli were manually removed by SCUBA divers from 0.25 m² quadrats that were randomly located on the sea bottom ($n = 10$). April (autumn) is when significant recruitment of *Undaria* occurs (Casas and Piriz 1996). Those quadrats were kept *Undaria*-free by monthly removal of sporophytes until the end of the experiment, by cutting the plants above the holdfast to avoid a mechanical impact on the other species. Another set of 0.25 m² quadrats in the same area were left intact and served as controls ($n = 10$). All quadrats were located, at least, 1 m from one another. The experiment was finished in December 2001, before summer senescence of *Undaria*, when all seaweeds were collected from all quadrats (Figure 2). Another way of testing for the effects of *Undaria* could have been to add *Undaria* thalli experimentally in pristine areas. However, such a procedure was discarded beforehand because of its potential danger, since *Undaria* was already known to be invasive. Taxa were identified in the laboratory as far down to the species level as possible. Blotted-dry wet biomass was separately determined for each taxon and for each quadrat to the nearest 0.01 g.

Species richness (S) was determined for each quadrat as the number of identified taxa (Krebs 1999). Species diversity, also known as species heterogeneity, was calculated for each quadrat using the Shannon–Wiener index (H'). This index is based on the proportional abundance of species and represents the probability of getting two different species in consecutive samples. When there is only one species present, H' is 0 and it increases
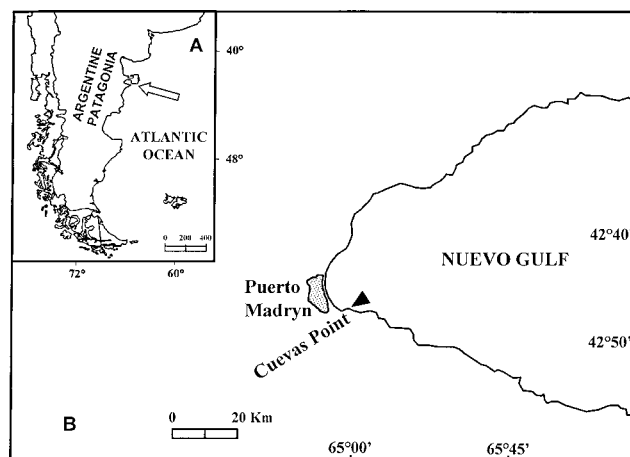

Figure 1. Map showing the location of the study site.

Figure 2. Manual removal of seaweeds at the end of the experiment.

as richness and evenness increase, reaching a peak when all species are equally abundant (Krebs 1999). Its mathematical expression is

$$H' = -\Sigma p_i \log_2 p_i,$$

where p_i is the proportion (in biomass) of a given species.

Evenness (E) indicates the degree of homogeneity in the distribution of species in a sample (Krebs 1999). It is calculated based on the ratio between the sample H' and the maximum possible H' (H'_{max}), which occurs when all species are equally abundant. E varies between 0, when the sample is dominated by one species, and 1, when all species are equally abundant. The evenness index was calculated for each quadrat as

$$E = H'(H_{max})^{-1} = H'(\log_2 S)^{-1}.$$

For the calculation of these three indices, *Undaria* was always excluded. Species richness, diversity, and evenness were compared between both treatments with independent *t*-tests. Data normality was verified with the Lilliefors test (Sokal and Rohlf 1981) and, when nonnormality occurred, data were logarithmically transformed before *t*-tests. Homoscedasticity was verified with Levene's test and, when heteroscedasticity occurred, Mann–Whitney's U test (Siegel 1980) was applied. Data analyses were done with Statistica 5.1 (StatSoft 1996).

Results

A total of 29 taxa were identified in this study, including 16 Rhodophyta, 8 Phaeophyceae, 4 Chlorophyta, and 1 colonial, tube-dwelling diatom (Table 1). However, only 14 taxa were common to both treatments.

Species richness (excluding *Undaria*) was 11 ± 1.5 (mean $\pm$ SE, $n = 10$) in the *Undaria*-removed quadrats and 4 ± 1.0 in the *Undaria*-present quadrats, which is a significant difference ($t = 3.97$, $P < 0.001$). The highest absolute richness (that is, in a single quadrat) was 19 taxa, and the lowest was 1 (only *Codium*).

Undaria was a dominant seaweed in the invaded areas, with an average biomass of 2882 ± 1175 g m^{-2} (mean $\pm$ SE, $n = 10$), representing an average of 65% of total seaweed biomass. The next most abundant species in the area was *Codium vermilara*, which was found in all quadrats and similarly abundant in both treatments in terms of biomass ($U = 42$, $P = 0.54$). Other frequent seaweeds in both treatments were *Polysiphonia argentinica*, *Ceramium rubrum*, *Dictyota dichotoma*, *Sphacelaria cirrosa*, *Ectocarpus siliculosus*, crustose Corallinaceae, *Lomentaria clavellosa*, *Streblocadia corymbifera*, *Ulva rigida*, and *Heterosiphonia merenia*.

The diversity or heterogeneity of native seaweeds, measured by the Shannon–Wiener index after excluding *Undaria* from calculations, was significantly higher ($U = 17$, $P = 0.013$) in *Undaria*-removed quadrats ($H' = 0.20 \pm 0.04$, mean $\pm$ SE, $n = 10$) than in *Undaria*-present quadrats ($H' = 0.07 \pm 0.04$).

The evenness index for native seaweeds (excluding *Undaria* from the analysis) was significantly higher ($U = 21$, $P = 0.028$) in *Undaria*-removed quadrats ($E = 0.06 \pm 0.01$, mean $\pm$ SE, $n = 10$) than in *Undaria*-present quadrats ($E = 0.03 \pm 0.02$), although the difference was actually low.

Discussion

In a worldwide study of 29 marine floras, the richness of the seaweed flora from Argentine Patagonia was classified as relatively poor (Bolton 1994). The 29 taxa identified in our study

Table 1. Wet biomass (g m^{-2}) and frequency of occurrence in samples (%) of taxa identified in both treatments ($n = 10$ for each treatment).

Taxa	*Undaria*-removed			*Undaria*-present		
	%	Mean	SE	%	Mean	SE
Acrochaetium sp.	20	0.008	0.005	0	0	0
Annotrichium furcellatum (J. Agardh) Baldock	20	0.008	0.005	0	0	0
Aphanocladia robusta Pujals	10	0.020	0.020	10	0.004	0.004
Bryopsis sp.	10	0.004	0.004	0	0	0
Callithamnion gaudichaudii C. Agardh	70	0.050	0.022	0	0	0
Ceramium rubrum (Hudson) C. Agardh	90	1.821	1.302	30	0.912	0.880
Ceramium strictum Greville *et* Harvey	20	0.012	0.010	0	0	0
Cladophora sp.	10	0.012	0.012	10	0.004	0.004
Codium vermilara (Olivi) Delle Chiaje	100	591.1	245.3	100	443.7	135.5
Colonial, tube-dwelling diatoms	30	0.012	0.006	0	0	0
Colpomenia sinuosa (Roth) Derbès *et* Solier	10	1.060	1.063	0	0	0
Crustose Corallinaceae	50	0.002	0.001	50	0.002	0.001
Dictyota dichotoma (Hudson) Lamouroux	90	4.912	1.702	40	1.101	0.733
Ectocarpus siliculosus (Dillwyn) Lyngbye	70	0.230	0.101	10	0.004	0.004
Eudesme virescens (Carmichael) J. Agardh	30	1.204	0.775	0	0	0
Gracilaria gracilis (Stackhouse) Steentoft, Irvine *et* Farnham	10	0.020	0.020	0	0	0
Heterosiphonia merenia (Reinsch) Falkenberg	40	0.201	0.094	10	0.004	0.004
Hymenena laciniata (Hooker fil. *et* Harvey) Kylin	10	0.184	0.184	0	0	0
Lomentaria clavellosa (Turner) Gaillon	50	0.440	0.280	10	0.004	0.004
Phycodrys quercifolia (Bory) Skottsberg	0	0	0	10	0.104	0.104
Polysiphonia argentinica Taylor	100	0.352	0.075	40	0.084	0.055
Polysiphonia brodiaei (Dillwyn) Greville	10	0.210	0.211	0	0	0
Scytosiphon lomentaria (Lyngbye) Link	20	0.064	0.044	0	0	0
Sphacelaria cirrosa (Roth) C. Agardh	90	0.164	0.040	20	0.008	0.005
Streblocladia camptoclada (Montagne) Falkenberg	10	0.004	0.004	10	0.008	0.010
Streblocladia corymbifera (C. Agardh) Kylin	50	0.140	0.080	10	0.004	0.004
Striaria attenuata Greville	10	0.004	0.004	0	0	0
Ulva rigida C. Agardh	50	3.061	1.772	30	0.110	0.070
Undaria pinnatifida (Harvey) Suringar	0	0	0	100	2881.6	1175.2
Species richness (*S*)		11	1.50		4	1.03
Diversity (*H'*)		0.20	0.04		0.07	0.04
Evenness (*E*)		0.06	0.01		0.03	0.02

represent 53% of the total amount collected during 1 year at three subtidal sites in Nuevo Gulf (M. L. Piriz and G. Casas, unpublished data). In terms of species richness, the values obtained in that study (14.4 ± 0.33, mean $\pm$ SE, $n = 93$) were similar to those of the present work in the *Undaria*-removed quadrats (11 ± 1.5, mean $\pm$ SE, $n = 10$).

This is the first study measuring the impact of the invasive kelp *Undaria pinnatifida* on the diversity of native seaweeds from Nuevo Gulf, where *Undaria* was first introduced in Argentina (Piriz and Casas 1994). The removal of *Undaria* from invaded sites resulted in a significant increase of native seaweed richness (*S*) and diversity (*H'*). Changes in the number of taxa were dramatic, as mean richness increased 175%. Our

removal experiment was a valid alternative to determine the potential seaweed richness and diversity that may have existed before the *Undaria* invasion, although perhaps more time after experimentally excluding *Undaria* might have allowed for a few more native species to settle. This information complements studies on the native seaweed flora from subtidal communities in Nuevo Gulf (M. L. Piriz and G. Casas, unpublished data).

The mechanisms behind the local spread and dominance of *Undaria* are unknown, although competitive exclusion involving light, nutrient, and substrate limitation and the lack of native herbivores preferentially feeding on *Undaria* are potential explanations (Shea and Chesson 2002). Understanding why *Undaria* is successfully

invading this region requires experimental research of those hypotheses and possibly of others that might result from more detailed observations. Other invasive seaweeds, such as species of *Caulerpa* (e.g. Ceccherelli and Cinelli 1999; Smith and Walters 1999; Ceccherelli and Piazzi 2001), are known to spread rapidly through vegetative fragmentation and reattachment of fragments elsewhere from the site of origin, but such mechanisms are not possible for *Undaria*.

The green alga *Codium vermilara* was, by far, the next most abundant seaweed after *Undaria*, and it seems to be resisting the *Undaria* invasion relatively well, as its biomass was statistically similar between both treatments. This species of *Codium* is considered the most common native subtidal seaweed in Nuevo Gulf (Olivier et al. 1966; Boraso de Zaixso et al. 1998; M. L. Piriz and G. Casas, unpublished data). Based on its competitive abilities and dominance, however, it has recently been suggested that *C. vermilara* might have been introduced to this region during the last 100 years (P. C. Silva, pers. commun.). This hypothesis deserves attention, since positive interactions between invasive species appear to facilitate their spread and dominance in other marine ecosystems (Levin et al. 2002).

In New Zealand, *Undaria pinnatifida* has also invaded coastal areas and dramatically reduced local biodiversity (Battershill et al. 1998). Our results and the international experience with *Undaria* invasions suggest that this species might continue to spread along the Patagonic coast. The consequences of such a process are potentially damaging, not only from a biodiversity viewpoint (Tilman 1999), but also from an economic perspective, as commercial species and/or their habitats might be negatively affected (Orensanz et al. 2002). For example, *Undaria* has recently been found in populations of the agar-producing red alga *Gracilaria gracilis* in Bustamante Bay, about 400 km south from Nuevo Gulf (H. García, pers. commun.). Efforts are currently being made to avoid its dispersal into commercial shellfish beds, a process that is suspected to be facilitated involuntarily by the management of fishing gear by local fishermen (Ciocco et al. 1998). Additionally, if the negative effects of *Undaria* on native seaweed biodiversity occur at all sites where *Undaria* invades in the future,

which is a likely event, the susceptibility of local benthic communities to future invasions by other species might ultimately increase (Kennedy et al. 2002; Stachowicz et al. 2002).

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