

Effects of the alien algae *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the diversity and abundance of benthic macrofauna in Golfo Nuevo (Patagonia, Argentina): potential implications for local food webs

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Abstract Changes in macroalgal community structure caused by invasive seaweeds have strong impacts on the associated macrofauna due to the role of macroalgae as autogenic ecosystem engineers. This study investigates the effect of *Undaria pinnatifida* on the abundance and diversity of benthic macrofauna in Golfo Nuevo, northern Patagonia, using a manipulative experiment involving the systematic removal of *Undaria* microthalli from strips of hard bottom during its eighth-month growing period. Species richness and diversity were higher in plots covered by *Undaria* than when *Undaria* was removed. Also, the abundance of two species of crustaceans, one species of sea urchin, one species of nemertina and several species of polychaetes was higher. We attribute these effects to the provision of new habitat structure by *Undaria*, a larger and structurally more complex species than the local native seaweeds. These results support the hypothesis that complex habitats enhance abundance

and species richness, by offering different shelter and foraging opportunities compared to morphologically simpler habitats. Based on a review of diet studies in the region, we speculate that *Undaria* could potentially produce a bottom-up effect on local food chains by increasing abundance of prey for a wide variety of predators, from invertebrates to marine mammals. While our study has a narrow temporal and spatial scale, we expect similar effects of *Undaria* on the macrofauna in other sites of the Argentine coast, especially those dominated by small native macroalgae.

Keywords Benthic macrofauna · Diversity · Invasive seaweed · *Undaria pinnatifida* · Food webs

Introduction

Seaweed invasions and eutrophication are among the most common anthropogenic impacts on coastal systems around the world (Kraufvelin and Salovius 2004; Lotze et al. 2006). Invasive species in most cases dominate native algal communities, while eutrophication increases primary production, inducing blooms of opportunistic algae capable of rapidly exploiting the elevated amounts of nutrients (Duarte 1995; Johnson 2007; Johnson and Chapman 2007). These processes produce changes in the structure of algal communities, and consequently in the associated

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benthic fauna (Buschbaum et al. 2006). The strong influence of marine macroalgae on benthic faunal communities is due to their role as autogenic ecosystem engineers: they add spatial complexity to the substrate and further modify a wide range of physical and environmental factors at a local spatial scale (Bolam and Fernandes 2002; Bolam et al. 2000; Chemello and Milazzo 2002; Forrest and Taylor 2002; Gribben and Wright 2006; Gribben et al. 2009; Schaffelke and Hewitt 2007; Schmidt and Scheibling 2007; Stuart 2004).

Undaria pinnatifida is native of northeast Asia (Japan, Korea and China) (Akiyama and Kurogi 1982). In 1971 it was found in l'Etang de Thau (France) and since then it has spread throughout the Mediterranean coasts and to other temperate waters around the world, mainly by shipping (Curiel et al. 1994; Fletcher and Manfredi 1995; Hay 1990; Salinas et al. 1996; Stegenga 1999). Since its introduction in Puerto Madryn, Argentina, in 1992, it first spread all over Golfo Nuevo, and has now reached sites 700 km south of the gulf's mouth on the outer coast, and recently managed to bypass (probably by shipping) the natural barrier represented by Península de Valdés, invading San José Gulf (Fig. 1) (Martin and Bastida 2008). With the exception of a few seasonal patches of *Macrocystis pyrifera* (Laminariales Laminariaceae) forests, most native species of macroalgae (e. g. *Codium* spp., *Dictyota* sp. and *Ulva* spp.) rarely exceed few centimetres in height (Eyras and Boraso 1994). The high densities of *Undaria* now observed along Golfo Nuevo have markedly changed the sea bottom landscape in waters between 0 and 15 m depth. Young *Undaria* sporophytes recruit in winter and grow rapidly to form dense forests between spring and early summer when plants reach a length of up to 2 m. The individuals begin to decompose in late spring, and their size progressively reduce until mid-autumn when hard bottoms become free of this algae (Casas et al. 2008). Golfo Nuevo belongs to the Peninsula Valdes area, listed as World Natural Heritage by the UNESCO in 1999. The conservation and management of this ecosystem are a big concern for both the public and private sectors. Yet, the impact of *Undaria* on local communities is unknown.

In this study we evaluate the effect of *Undaria* on the diversity and abundance of hard-bottom benthic macrofauna via a manipulative experiment in which we kept strips of sea bottom free of *Undaria* during

its eighth-month growing period. In order to discuss potential bottom-up effects of the changes induced by *Undaria* we review regional diet studies to assess the relative importance of the taxa associated with *Undaria* as prey for other species.

Materials and methods

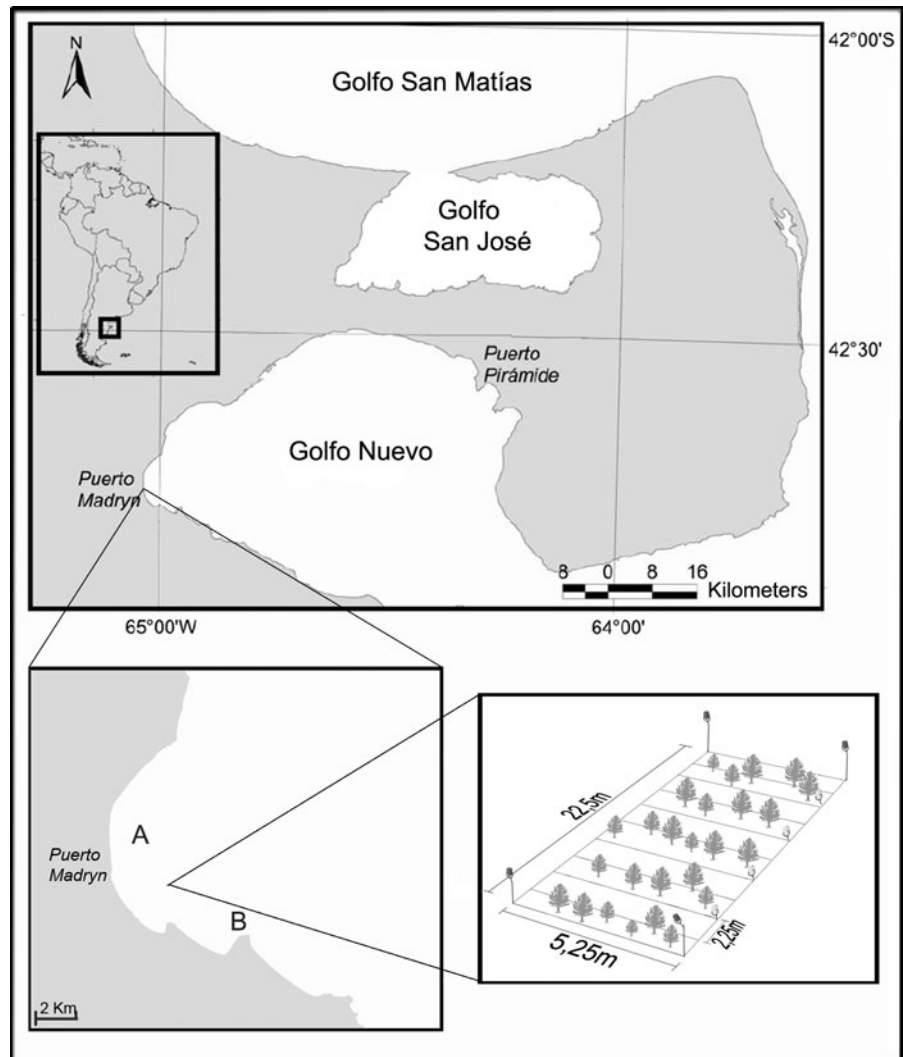
Study site

The field study was conducted close to Punta Cuevas, Golfo Nuevo (Fig. 1), on a relatively flat area occupied by limestone platforms and sandy patches. The hard bottoms (limestone platforms) are dominated by *Codium* spp., *Dictyota* sp, *Ulva* spp., the mussel *Aulacomya atra atra* and, since 2000, by dense seasonal forests of *Undaria pinnatifida*. Punta Cuevas was chosen because it is an accessible area.

Sampling design

An experimental grid consisting of 10 contiguous strips (2.25 m × 5 m) was set up in April 2008 on a limestone platform, at a depth that varied between 6 m at low tide and 11 m at high tide. *Undaria* sporophytes were systematically removed on every other strip starting in June 2008 when sporophytes begin to recruit. The final set up consisted of alternated strips of *Undaria*-removed and *Undaria*-intact treatments (Fig. 1), resulting in 5 replicates per treatment. On each removal event all microthalli (young sporophytes <15 cm) that had grown on the *Undaria*-removed strips were detached from the holdfast with a knife. After 8 months (December 2008), one 0.5-m² quadrat was randomly placed within each strip (separated by more than 0.5 m from the borders) and all benthos was collected manually or with an iron spatula and stored in a mesh bag (0.5 mm). *Undaria* individuals with their associated fauna (from *Undaria*-intact samples) were collected in a separate mesh bag in order to distinguish the macrofauna directly associated to the plants from the rest. Samples were refrigerated and all macrofauna (defined as animals visible to the naked eye) were identified to the lowest possible taxonomic level in the laboratory. Finally, the surface area occupied by *Undaria* was estimated by measuring the holdfasts area in the laboratory.

Fig. 1 Map of Peninsula Valdes in North Patagonia, Argentina, showing the location of the study site, Punta Cuevas, and the location and a scheme of the experimental grid consisting of ten contiguous strips (2.25 m × 5 m) of alternating *Undaria*-intact and *Undaria*-removed treatments



Data analysis

To assess the effect of *Undaria* on macrofauna diversity we first calculated species richness S and the “Shannon-Wiener” diversity index H' (Krebs 1989), according to:

S = number of taxa found

$$H' = - \sum_{i=1}^S p_i \text{LOG}_{10}(p_i)$$

where p_i = proportion of the total number of individuals in the sample belonging to i -th species.

The significance of the difference between samples with and without *Undaria* for each of the indices and for the abundance (=number of individuals) of

each of the taxa was evaluated using a t -test, treating *Undaria* as fixed factor (Levels: removed and intact). Normal distribution and homogeneity were verified by homogeneity tests (Bartlett and Levene tests) and residual plots. All analyses were performed with the R software (R Development Core Team 2007).

To further illustrate differences in the diversity between treatments, we used rank-abundance plots, in which the logarithm (base 10) of each p_i value was plotted against the species' rank, from the most to the least abundant (Feisinger 2001).

Potential implications on local food webs

A bibliographic review of diet studies conducted in north and central Patagonia (from 42°S to 45°S) was

used to evaluate the relative importance of the taxa found in the samples as prey of other species. Only taxa for which it was possible to compare abundance between treatments were considered (see “Results”). The occurrence of each taxa (% of analyzed stomachs or pellets in which the item was present) in the diet of each of the predators was classified into four arbitrary categories: $x = 0-2.5$, $xx = 2.5-10$, $xxx = 10-25$ and $xxxx = 25-100$.

Results

Samples with *Undaria* had an average of 2.4 ± 1 sporophytes (mean \pm standard deviation), $1,308 \pm 571$ g of wet weight and a total holdfast area of 295 ± 107 cm² covering $11\% \pm 4\%$ of the total area of the samples (2,500 cm²). The total wet weight of native species of seaweeds (mostly *Codium fragile*, *Dictyota dichotoma* and *Ulva* spp.) was 120 ± 73 and 290 ± 120 g (mean \pm standard deviation) in *Undaria*-intact and *Undaria*-removed samples, respectively.

The presence of *Undaria* was associated with increased species richness and diversity. We found statistically significant differences for the species richness (S) and the Shannon-Wiener (H') index (Table 1). Moreover, the rank-abundance graphs show that, despite the fact that both treatments are dominated by the same three taxa (*Aulacomya atra atra*, *Tegula patagonica* and polychaetes in the family Eunicidae), the dominance is lower in *Undaria*-intact samples. Furthermore, taxa of intermediate and low abundance had more evenness and richness on samples with *Undaria* (Fig. 2). We registered a total of 29 taxa, 26 in samples with *Undaria*-intact and 20 in samples with *Undaria*-removed. Nine taxa were found only in samples with *Undaria* and three were found only in samples without *Undaria* (Table 1). To our knowledge all taxa found are native species.

On 16 of the 29 taxa abundance was high enough to allow comparisons between treatments: the crabs *Coenophthalmus tridentatus* and *Leucippa pentagona*, the shrimp *Nauticaris magellanica*, the sea urchin *Arbacia dufresnii*, the mussel *Aulacomya atra atra*, the chitons *Chaetopleura isabellei* and *Plaxiphora aurata aurata*, the lamp *Fissurella radiosa tixierae*, the snail *Tegula patagonica*, the ophiuroidea

Ophioplocus janarii, the Nemertina (Hineidae Neolineus) and four polychaete families (Eunicidae, Nerididae, Glyceridae, Flabelligeridae and Polynoidae). Polychaetes were analyzed as a group as were chitons (*Chaetopleura isabellei* and *Plaxiphora aurata aurata*). In the case of the mussel *Aulacomya atra atra*, recruits (<8 mm) were discriminated from adults and analyzed separately.

Abundance was significantly higher in the samples with *Undaria* for the following taxa: the crustaceans *Coenophthalmus tridentatus* and *Nauticaris magellanica*, the sea urchin *Arbacia dufresnii*, the Nemertina (Hineidae Neolineus) and the polychaetes. The taxa that did not show significant differences were the crustacean *Leucippa pentagona*, the mussel *Aulacomya atra atra* (recruits and adults), the limpet *Fissurella radiosa tixierae*, the snail *Tegula patagonica*, the ophiuroidea *Ophioplocus janarii* and the chitons (*Chaetopleura isabellei* and *Plaxiphora aurata aurata*) (Fig. 3).

The shrimp *N. magellanica* was found only in samples with *Undaria* and directly associated to the holdfasts and sporophylls. In the case of the crab *C. tridentatus*, only one individual was directly associated to the *Undaria* structure, but all the others were found beneath *Undaria* fronds. The crab *L. pentagona*, the ophiuroidea *O. janarii* and the limpet *F. radiosa tixierae* were approximately twice more abundant in *Undaria* samples, but this difference was not statistically significant due its high variability. Larger samples or more replicates would be necessary for the assessment of these highly variable species.

All species of polychaete found in the samples were exclusively mobile species that depend on biogenic or abiotic refuges to live. 60% of the individuals collected in *Undaria*-intact samples were found inside the holdfasts.

The Nemertina showed contrasting abundance between treatments ($n = 13$ in *Undaria*-intact vs. 1 in *Undaria*-removed treatments), but only 6 of the 13 individuals were found directly associated to the algae.

Finally, the sea urchin *Arbacia dufresnii* showed markedly dissimilar abundances between treatments.

Despite the lack of information on diet of regional marine fauna, especially on fishes, we could list a wide range of predators for the macrofauna present in the samples, including species of high tropic level (Bigatti et al. MS-a, MS-b; Galván 2008;

Table 1 Taxa sampled in quadrats from strips with *Undaria*-intact and *Undaria*-removed treatments

Phylum	Family	Species/sample	N											
			N with <i>Undaria</i>					N without <i>Undaria</i>					With <i>Undaria</i>	Without <i>Undaria</i>
			1	2	3	4	5	6	7	8	9	10		
Mollusca	Mytilidae	<i>Aulacomya atra atra</i>	795	558	521	836	624	816	628	625	750	740	3334	3559
Mollusca	Trochidae	<i>Tegula patagonica</i>	62	61	64	93	83	78	78	41	95	100	363	392
Annelida	Neritidae	–	25	29	16	46	28	8	16	0	7	33	144	64
Echinodermata	Arbaciidae	<i>Arbacia diufresnii</i>	2	8	9	7	11	1	4	1	2	3	37	11
Crustacea	Hippolytidae	<i>Nauticaris magellanica</i>	5	0	6	3	6	0	0	0	0	0	20	0
Echinodermata	Ophiuridae	<i>Ophioplocus janarii</i>	6	2	5	2	5	4	0	0	3	4	20	11
Annelida	Eunicidae	–	2	3	0	7	3	2	0	1	3	0	15	6
Nemertina	Hineidae	<i>Neolineus</i>	0	4	4	2	3	0	0	1	0	0	13	1
Mollusca	Fissurellidae	<i>Fissurella radiosa tixierae</i>	0	2	4	1	1	1	0	1	2	0	8	4
Crustacea	Portunidae	<i>Coenophthalmus tridentatus</i>	2	0	2	2	1	1	0	0	0	0	7	1
Crustacea	Majidae	<i>Leucippa pentagona</i>	0	0	5	2	0	0	0	2	1	1	7	4
Annelida	Polynoidae	–	1	0	3	1	1	0	0	0	2	1	6	3
Mollusca	Ischnochitonidae	<i>Chaetopleura isabellei</i>	2	0	3	0	0	2	0	1	0	3	5	6
Crustacea	Hymenosomatidae	<i>Halicarcinus planatus</i>	0	0	0	1	1	0	0	0	0	1	2	1
Mollusca	Murucidae	<i>Trophon geversianus</i>	0	1	1	0	0	0	0	1	0	0	2	1
Mollusca	Ischnochitonidae	<i>Plaxiphora aurata aurata</i>	0	0	0	2	0	0	1	0	0	2	2	3
Sipuncula	–	–	0	1	1	0	0	0	0	0	0	0	2	0
Annelida	Glyceridae	–	1	0	0	0	1	0	0	0	0	0	2	0
Urochordata	–	–	1	1	0	0	0	0	0	0	0	0	2	0
Cnidaria	–	–	2	0	0	0	0	0	0	0	0	0	2	0
Echinodermata	Asteridae	<i>Anasterias minuta</i>	0	1	0	0	0	0	0	0	0	0	0	0
Echinodermata	Asteridae	<i>Allotichaster capensis</i>	0	0	1	0	0	0	0	1	1	0	2	2
Mollusca	Epitonidae	<i>Epitonium georgettiniae</i>	1	0	0	0	0	0	0	0	0	0	0	0
Mollusca	Pectinidae	<i>Aequipecten tehuelchus</i>	1	0	0	0	0	0	0	0	1	0	1	1

Table 1 continued

Phylum	Family	Species\sample	N with Undaria										N without Undaria										N	With Undaria	Without Undaria
			1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10			
Mollusca	Mytilidae	<i>Musculus vitor</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platyhelminthes	-	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca	Buccinidae	<i>Pareuthria powelli</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mollusca	Veneridae	<i>Tivela isabelleana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Annelida	Flabelligeridae	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>N total</i>	909	671	646	1005	768	913	727	675	869	889	3999	4073													
<i>S richness</i>	16	12	16	14	13	9	5	10	13	11	26	20													
<i>H' Shannon-Wiener index</i>	0.249	0.299	0.366	0.297	0.3325	0.185	0.212	0.142	0.229	0.273	0.311318955	0.218939897													
Phylum	Family	Species\sample	Occurrence (%)		N directly associated to Undaria (%)		“t” test																		
			With Undaria	Without Undaria	t _{1,8}	P _{≤0.05}																			
Mollusca	Mytilidae	<i>Aulacomya atra atra</i>	100	100	25	0.24/1.23	0.8/0.23 ns																		
Mollusca	Trochidae	<i>Tegula patagonica</i>	100	100	20	6.73	0.65 ns																		
Annelida	Neritidae	-	100	80	60	2.36	0.046*																		
Echinodermata	Arbaciidae	<i>Arbacia dufrsenii</i>	100	100	40	3.22	0.022*																		
Crustacea	Hippolytidae	<i>Nauticaris magellanica</i>	80	0	100	3.58	0.024*																		
Echinodermata	Ophiuridae	<i>Ophioplocus janarii</i>	100	60	15	1.45	0.18 ns																		
Annelida	Eunicidae	-	80	60	60	2.36	0.046*																		
Nemertina	Hineidae	<i>Neolineus</i>	80	20	47	3.01	0.03*																		
Mollusca	Fissurellidae	<i>Fissurella radiosa tixierae</i>	80	60	50	1.06	0.33 ns																		
Crustacea	Portunidae	<i>Coenophthalmus tridentatus</i>	80	20	28	2.68	0.0378*																		
Crustacea	Majidae	<i>Leucippa pentagona</i>	40	60	85	0.58	0.58 ns																		
Annelida	Polynoioidae	-	80	40	60	2.36	0.046*																		
Mollusca	Ischonochitonidae	<i>Chaetopleura isabellei</i>	40	60	50	0.14	0.71 ns																		
Crustacea	Hymenosomatidae	<i>Hallicarcinus planatus</i>	20	20	50	-	-																		
Mollusca	Murucidae	<i>Trophon geversianus</i>	40	20	0	-	-																		
Mollusca	Ischonochitonidae	<i>Plaxiphora aurata aurata</i>	20	40	50	0.14	0.71 ns																		
Sipuncula	-	-	40	0	50	-	-																		
Annelida	Glyceridae	-	40	0	60	2.36	0.046*																		

Table 1 continued

Phylum	Family	Species/sample	Occurrence (%)		N directly associated to <i>Undaria</i> (%)	“t” test	
			With <i>Undaria</i>	Without <i>Undaria</i>		t _{1,8}	P _{<=0.05}
Urochordata	–	–	20	0	100	–	–
Cnidaria	–	–	20	0	100	–	–
Echinodermata	Asteriidae	<i>Anasterias minuta</i>	20	0	0	–	–
Echinodermata	Asteriidae	<i>Allotichaster capensis</i>	20	40	0	–	–
Mollusca	Epitonidae	<i>Epitonium georgettiniae</i>	20	0	100	–	–
Mollusca	Pectinidae	<i>Aequipecten tehuelchus</i>	20	20	0	–	–
Mollusca	Mytilidae	<i>Musculus vitator</i>	20	0	0	–	–
Platyhelminthes	–	–	20	0	100	–	–
Mollusca	Buccinidae	<i>Pareuthria powelli</i>	0	20	0	–	–
Mollusca	Veneridae	<i>Tivela isabelleana</i>	0	20	0	–	–
Annelida	Flabelligeridae	–	0	20	60	–	–
“t” test							
<i>S richness</i>							
<i>H' Shannon-Wiener index</i>							
						t _{1,8}	P _{<=0.05}
						2.96	0.022*
						3.04	0.0092**

Number of individuals, occurrence (percent of samples where species was present). Species richness (S) and Shannon-Wiener index (H') for each sample and total for each treatment. “t” student coefficients and values of p_{>=0.05} shown for comparisons of S, H' and abundance of reef fish preys

Significance of the differences between abundance of taxas, species richness S and the “Shannon-Wiener” diversity index on samples with and without *Undaria* is indicated by: * significant, ** high significant, *** highly significant and ns no significant

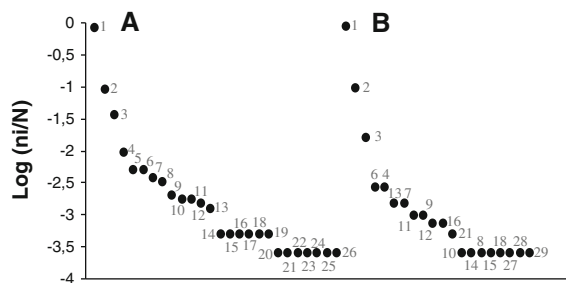


Fig. 2 Proportion of species in samples of *Undaria*-intact (A) and *Undaria*-removed (B) treatments. Species ordered from most to least abundant in the “x” axis discriminated by treatment: (1) *Aulacomya atra atra*, (2) *Tegula patagonica*, (3) Polichaeta (Nerididae), (4) *Arbacia dufresnii*, (5) *Nauticaris magellanica*, (6) *Ophioplocus janarii*, (7) Polichaeta (Eunicidae), (8) Nemertina (Hineidae, Neolineus), (9) *Fissurella radiosa tixierae*, (10) *Coenophthalmus tridentatus*, (11) *Leucippa pentagona*, (12) Polichaeta (Polinoxyidae), (13) *Chaetopleura isabellei*, (14) *Halicarcinus planatus*, (15) *Trophon geversianus*, (16) *Plaxiphora aurata aurata*, (17) Nemertina, (18) Polichaeta (Glyceridae), (19) Cnidaria, (20) *Anasteria minuta*, (21) *Allotichaster capensis*, (22) *Epitonium georgettiniae*, (23) *Aequipecten tehuelchus*, (24) *Musculus viator*, (25) *Platyhelminthes*, (26) Urochordata (Ascidia), (27) Polichaeta (Flabelligeridae), (28) *Tivela isabelleana*, (29) *Pareuthria powelli*

Galván et al. 2009; Gosztanyi and Kuba 1998; Herrera et al. 2005; Hidalgo et al. 2007; Ré et al. 2006; Sapoznikow 2006; Yorio and Bertellotti 2002): two species of gastropods, five of fishes, two of octopus, five sea birds and the sea lion *Ottaria flavescens* (Table 2). Furthermore, among the most commonly consumed species were those found in increased abundance in the presence of *Undaria*, as was the case of polychaetes and crustaceans. In addition, we found that some predators are important prey of other predators. For example, *Octopus tehuelchus* is an important prey of the cormorants (especially of *Phalacrocorax magellanicus*) while the two octopus species and reef fishes are common preys of *Ottaria flavescens*. The macrobenthic fauna from hard bottoms seems to play an important role in the diet of reef fishes, octopus species and cormorants: reef fishes and octopuses inhabit hard bottoms and cormorants are coastal divers which forage on subtidal hard bottoms. On the other hand, the sea lion *Ottaria flavescens* rarely prey on taxa analyzed in this study (only 1.6% of polychaetes occurrence was found on its diet), however octopuses and reef fishes are of main importance for the species.

Discussion

Worldwide, there has been a lack of information on the impact of alien macroalgae on native faunal communities (Wotton et al. 2004). Our work focuses on the effects of *Undaria* on the abundance and diversity of benthic macrofauna in Golfo Nuevo, northern Patagonia. We showed that the presence of *Undaria* is associated with increased species richness and diversity, and could potentially produce a bottom-up effect on local food chains by increasing the abundance of preys for a wide range of predators. Although we could not confirm that the increasingly abundant preys in *Undaria*-colonized habitats are available to predators during *Undaria*'s growing season, they certainly become available when sporophytes decompose during the summer.

Cryptic taxa of macrofauna (i.e. dependent on biogenic or abiotic refuges to live) collected in *Undaria*-intact samples were found mostly inside holdfast and sporophylls of *Undaria* (100% of the shrimps, 60% of the polychaetes and 47% of the nemertines). Considering that *Undaria* occupy on average 11% of the sampled area, we attribute the differences in abundance between treatments to an increase in the availability of refuges offered by *Undaria*. Furthermore, mobile taxa which depend on biogenic or abiotic refuges or substrates to live were also found mostly associated with *Undaria* (e.g. 85% of the crabs *Leucippa pentagona*, 50% of the lamps *Fissurella tixierae*, 40% of the sea urchin *Arbacia dufresnii* and 28% of the crabs *Coenophthalmus tridentatus*). In the case of sessile organisms (ascidians and cnidarians), they were found exclusively attached to *Undaria* fronds. These results support the hypothesis that the effects of *Undaria* on the native macrofauna assemblage are principally due to its character of bioengineer. Complex habitats provide different shelter and foraging opportunities than morphologically simpler habitats (Forrest and Taylor 2002; Schmidt and Scheibling 2007). The lack of effects of *Undaria* on mussels and chitons, which settle on hard substrates, reinforces this conclusion.

In addition to the habitat-forming effect of *Undaria*, this algae is a food resource for some species and could potentially enhance consumer populations. Recently, the green sea urchin and the snail tegula were identified as *Undaria* consumers. These herbivore species consume *Undaria* mainly during the senescent period

Fig. 3 Mean abundance \pm standard error of taxa in samples with *Undaria* intact (grey bars) and *Undaria*-removed treatments (white bars)

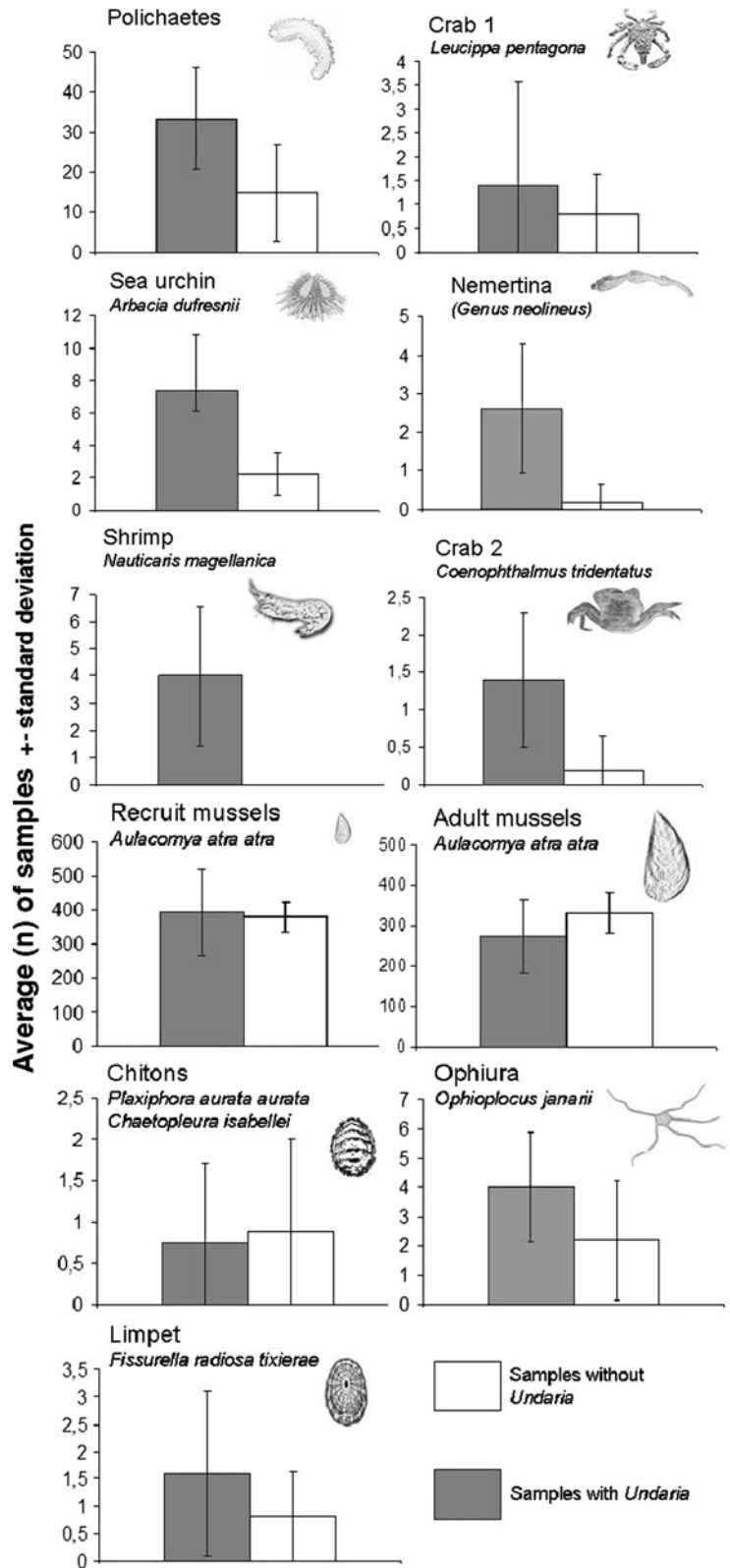


Table 2 Predator species and prey taxa

Predator/Prey	Annelida*	Echinodermata Arbaciidae <i>A. dufresnii</i>	Crustacea Hippolytidae <i>N. magellanica</i>	Crustacea Portunidae <i>C. iridentatus</i>	Mollusca Fissurellidae <i>F. radiosa</i> <i>rixterae</i>	Crustacea Majidae <i>L. pentagona</i>	Mollusca Mytilidae <i>A. atra</i> <i>T. patagonica</i>	Mollusca Trochidae <i>T. patagonica</i>	Mollusca Ischonoichitoniidae	Reference
Gastropods										
1 <i>Adelomelon ancilla</i>	–	X	–	–	–	–	XX	XX	–	Bigatti et al. MS-b
2 <i>Odontocymbiola magellanica</i>	–	–	–	–	–	–	X	XXXX	–	Bigatti et al. MS-a
Reef fishes										
3 <i>Patagonotothen cornucola</i>	XXX	–	–	–	–	–	–	–	–	Hidalgo et al. (2007)
4 <i>Pingipes brasiliannu</i> ³	XXX	XXXX	–	X	X	XX	XXX	–	XX	Galván (2008–2009)
5 <i>Pseudoperis semisfasciata</i> ^{2, 3, 4, 6, 7 and 8}	XX	X	X	X	XXX	–	X	–	–	Galván (2008–2009)
6 <i>Acanthissius patachonicus</i> ^{3, 4 and 7}	XXX	X	–	X	–	–	X	–	–	Galván (2008–2009)
Octopods										
7 <i>Octopus tehuelchus</i> ³	XXX	–	–	–	–	X	–	–	X	Ré Unpublished data
8 <i>Enteractopus megalocyathus</i> ^{3 and 7}	XXX	–	XX	–	–	–	–	–	–	Ré et al. (2006)
Sea birds										
9 <i>Larus dominicanus</i>	XX	X	–	–	X	XX	X	X	XXX	Yorio and Bertelotti (2002)
10 <i>Larus atlanticus</i>	XX	–	–	–	–	XX	–	–	–	Herrera et al. (2005)
11 <i>Phalacrocorax atriceps</i> ^{3, 4, 5, and 6}	X	–	X	–	–	–	–	–	–	Gosztonyi and Kuba (1998)
12 <i>Phalacrocorax albiventer</i> ^{4, 6 and 7}	XXXX	–	–	–	–	–	–	–	–	Malacalza et al. (1994)
13 <i>Phalacrocorax magellanicus</i> ^{3 and 7}	XXXX	–	XX	–	–	–	–	–	–	Sapoznikow (2006)
Marine mammals										
14 <i>Otaria flavescens</i> ^{3 to 8}	X	–	–	–	–	–	–	–	–	Koen et al. (1999)

Percent occurrence discriminated by four categories: x = 0–2.5, xx = 2.5–10, xxx = 10–25, xxxx = 25–100

The numbers on the right of the predators' name show the identifier of predators which are also prey

* Annelida include Eunicidae, Neritidae and Polynoidea families

(December to April), when the algae is palatable (Teso et al. 2009). Differences would be larger later in the season when high densities of *T. patagonica* can be observed covering the whole structure of *Undaria*. Other consumer species likely exist but have not been identified yet. For example, when *Undaria* is highly decomposed (during the summer) dense concentrations of small crustaceans (probably isopods and amphipods) are frequently observed associated with *Undaria* (personal observations).

Unfortunately, the logistic complications associated with maintaining the removal experiments given the prevailing rough weather and strong winds in Patagonia restricted the scale of the experiment. While we acknowledge that the narrow temporal and spatial scale of our study precludes generalizing our conclusions, we expect to observe similar effects of *Undaria* on the macrofauna in other sites of the Argentine coast, especially on sites dominated by small native macroalgae.

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