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Distribution of *Sargassum muticum* on the North West coast of Spain: Relationships with urbanization and community diversity

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ABSTRACT

Invasions are common in coastal marine environments where proximity to urban areas should influence the number of non-native organisms due to the likelihood of unintentional introductions from urban centers. Invasive species are widely recognised as important agents of global change, and can colonize new habitats and even cause local extinction of native species. This study was focused on the invasive marine macroalga *Sargassum muticum*, a problematic invasive species on the West coast of America and in European waters. An intensive survey was carried out along the Galician coast (North West of Spain) from March to August 2008 to determine the current distribution of this species, and its relationship with level of urbanization and native macroalgal diversity. We sampled the presence of *S. muticum* and native macroalgae in the mid and low intertidal zones of twenty rocky shores distributed along ten rias. Rias were grouped into high and scarcely urbanized based on their population density. Results indicated that *S. muticum* was present in nine out of the ten rias, confirming its presence in most of the intertidal rocky shores of Galicia twenty years after it was first observed. The presence of *S. muticum* was not related to the degree of urbanization of the rias, and its distribution and abundance did not seem to be influenced by diversity or functional groups of native algae. In addition, there was a great variability in the percentage cover, number and length of individuals amongst localities and rias suggesting that both large-scale and local processes may play a role in the distribution of this species. This study highlights the importance of future research into the distribution and impact of introduced algae and proves the urgent need for monitoring programmes and increasing efforts to prevent and control new introductions.

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1. Introduction

The number of species anthropogenically introduced outside their natural ranges is rapidly increasing (Levine et al., 2003). After loss of habitat, non-native species are the second leading cause of biodiversity loss, particularly in freshwater ecosystems (Vitousek et al., 1997; Mack et al., 2000). Besides imposing huge economic costs, invasive species may cause extinction of native species, reduction of genetic diversity and biotic homogenization through a variety of mechanisms (Pimentel et al., 2000). The high environmental and economic costs resulting from introduction of non-native species have generated a significant increase in research to assess potential impacts, factors affecting invasions and the distribution of non-native species over

different spatial and temporal scales (e.g. Stachowicz et al., 2002; Pauchard and Shea, 2006).

The invasion process can be categorised broadly into four sequential distinct stages: the introduction or arrival of propagules at a site beyond their previous geographical range, the colonization, the establishment of a self-sustaining population within their new non-native range and the spread or diffusion (Theoharides and Dukes, 2007), when typically non-native species become invasive and eventually cause some ecological or/and economic harm. At any of these stages, from propagule dispersal to production of new propagules, non-native species face diverse ecological constraints (i.e. competitive resistance, herbivory or availability of resources) that are spatial-scale dependent (Pauchard and Shea, 2006). Observational studies focused on spatial and temporal patterns of distribution of non-native species may contribute to make hypotheses on the possible processes regulating invasiveness and thus help us to identify more efficient and effective control strategies.

Invasions are an increasing phenomenon in coastal marine environments, where embayments and estuaries appear to be more prone to introductions than open coast habitats (Carlton,

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1996). Ports and harbours are primary points of inoculation and may also serve as “hubs” for the transport of non-native species to nearby locations (Hewitt et al., 2004). Native species are also affected by coastal development or urbanization (see Mangialajo et al., 2008). In fact, it has been shown that the decrease in the number of native species is amongst the most important consequences linked to the alteration of the landscape by human activity, especially by urbanization or human population density (Kennard et al., 2002; Marchetti et al., 2004). On the one hand, non-native species richness increases with level of urbanization due to the likelihood of unintentional introductions from urban centers and on the other hand, coastal development provokes the loss of diversity of native communities, mainly due to the degradation of water quality (Airoldi and Beck, 2007). Apart from urbanization, intrinsic characteristics of recipient communities, such as identity of native species, diversity, frequency of disturbance or availability of resources have been invoked as important factors determining invasion success (Elton, 1958; Stachowicz et al., 2002; White and Shurin, 2007). In fact, the relationship between community diversity and invasibility has been a subject of on-going debate in ecology. One of the earliest generalizations and more persistent conceptual paradigms to explain the establishment success of non-native species was the concept of “biotic resistance” proposed by Elton (1958) that predicts that highly diverse communities should be less susceptible to invasion because of a more complete utilization of resources. This hypothesis has received much recent attention, primarily in the form of experimental studies with terrestrial plants and surveys comparing the number and abundance of non-native species with native diversity. Nevertheless, there is a lack of consensus on the strength and direction of the effects of diversity on community resistance to invasion.

Seaweeds are a significant component of invasions in coastal habitats, representing about 5% of the total flora (Ribera and Bouderesque, 1995) and about 10–40% of the total alien species (Schaffelke et al., 2006). Introduced seaweeds have often been associated with changes in biodiversity and community structure by monopolizing space, changing food webs or competing for resources (Stachowicz et al., 2002; Scheibling and Gagnon, 2006). Despite potential impact of seaweeds on coastal communities, few species have been studied in detail and information on their ecological, evolutionary and economic impacts is sparse compared with other taxa. In particular, information on the area occupied by most invasive seaweeds is lacking. In most cases, monitoring studies have been conducted at small to intermediate spatial scales, such as within patches or bays (Lyons and Scheibling, 2009).

Sargassum muticum (Yendo), a brown canopy forming macroalga originated from Asia, is considered one of the most aggressive of the marine macroalgal invaders (Bouderesque and Verlaque, 2002). It was introduced to North America in the 1940s and to Europe in the early 1970s (Critchley et al., 1983) probably attached to imported Japanese oysters (*Crassostrea gigas*) (Scagel, 1956). It has subsequently spread along the Atlantic coast of Western Europe from Scandinavia in the north to Portugal in the south (Rueness, 1989; Karlsson and Loo, 1999). This species occupies mainly sheltered shores where it forms dense monospecific canopies spanning lower intertidal, including tide pools, to subtidal regions (Critchley et al., 1983; Fernández et al., 1990). On the Iberian Peninsula coast, the presence of *S. muticum* was first reported from Asturias in the 1980s and subsequently it was observed on the Galician coast in 1986 (see Pérez-Cirera et al., 1989). Since then, a strong interest has been arisen to understand the biotic and abiotic interactions that mediate the establishment and spread of *S. muticum* and its interaction with native marine communities (Sánchez and Fernández, 2006; Incera et al., 2009;

Olabarria et al., 2009a, b). For example, previous studies found that functional group diversity and diversity of native communities are important factors regulating the invasion of *S. muticum*, but with contrasting effects on different stages of invasion (Britton-Simmons, 2006; White and Shurin, 2007). Different functional groups such as crustose and turfy algae inhibited *S. muticum* recruitment, whereas canopy and understory algae reduced *S. muticum* survivorship (Britton-Simmons, 2006).

Yet there is very little information about the spatial distribution of *S. muticum* along the Galician coast. The aim of this study was to determine the present status and distribution of *S. muticum* on the Galicia coast (North West of Spain) and its relationship with an anthropogenic disturbance such as urbanization, and the diversity of native macroalgal communities. We expected a better establishment (measured as percentage cover, biomass, number and length of individuals) in more urbanized rias due to more appropriate conditions to invasion success originated from anthropogenic impacts (i.e. marinas, harbours, pollution, physical disturbance) and due to a smaller diversity of native macroalgal communities than in scarcely urbanized rias. In addition, we expected the different functional groups of native macroalgae to play a role in shaping the pattern of distribution and abundance of *S. muticum*.

2. Material and methods

2.1. Sampling design

The study was done on the intertidal rocky shores of 10 rias located along the Galician coast (NW Spain) from March 2008 to August 2008 (Fig. 1). The Galician rias are a set of prolonged inlets in the shore distributed over 1720 km of the Iberian coast. They are considered to have several sectors: the ria itself is divided into inner and outer zones, according to their hydrodynamic and sedimentologic characteristics. The outer zone is located in the rias mouth, sometimes protected from direct oceanic influence by islands. The estuary is close to the head of the ria, where the principal river flows into it, although there may also be an estuary system in the secondary fluvial outflow channels (Méndez and Vilas, 2005). A variety of intensive human activities impact the rias and their surroundings, including harbours, industrial complexes, buildings, agriculture and livestock exploitations.

Based on data from the National Statistics Institute of Spain (INE, www.ine.es), rias were grouped into highly urbanized rias (HUR) (> 100 inhabitants/km²) and scarcely urbanized (SUR) (< 100 inhabitants/km²). The HUR group was formed by the Ria de Coruña (5163.1 inhabitants/km²), Ferrol (809.7 inhabitants/km²), Vigo (545.2 inhabitants/km²), Pontevedra (224.4 inhabitants/km²) and Arousa (105.3 inhabitants/km²) and the SUR group was formed by the Ria de Cedeira (80.4 inhabitants/km²), Ares-Betanzos (69 inhabitants/km²), Muros (62.6 inhabitants/km²), Camariñas (41.5 inhabitants/km²) and Corcubión (16.6 inhabitants/km²).

Within each ria, two localities about 30–50 m long and at least 5 km apart, were selected, one in the inner and one in the outer part, respectively. Within each locality, 5 plots of 50 × 50 cm were randomly distributed at a distance of at least 3 m from each other at two levels on the shore, the mid (1–1.5 m above the lowest astronomical tide) and the low (0.4–0.8 m above the lowest astronomical tide) intertidal levels.

In each plot the percentage cover of *S. muticum* (when it was present) and other macroalgae was quantified visually using a 50 × 50 cm metallic quadrat, subdivided into 25 sub-quadrats of 10 × 10 cm each, and a score from 0% to 4% was given to each taxon in each sub-quadrat after visual inspection. Final cover was

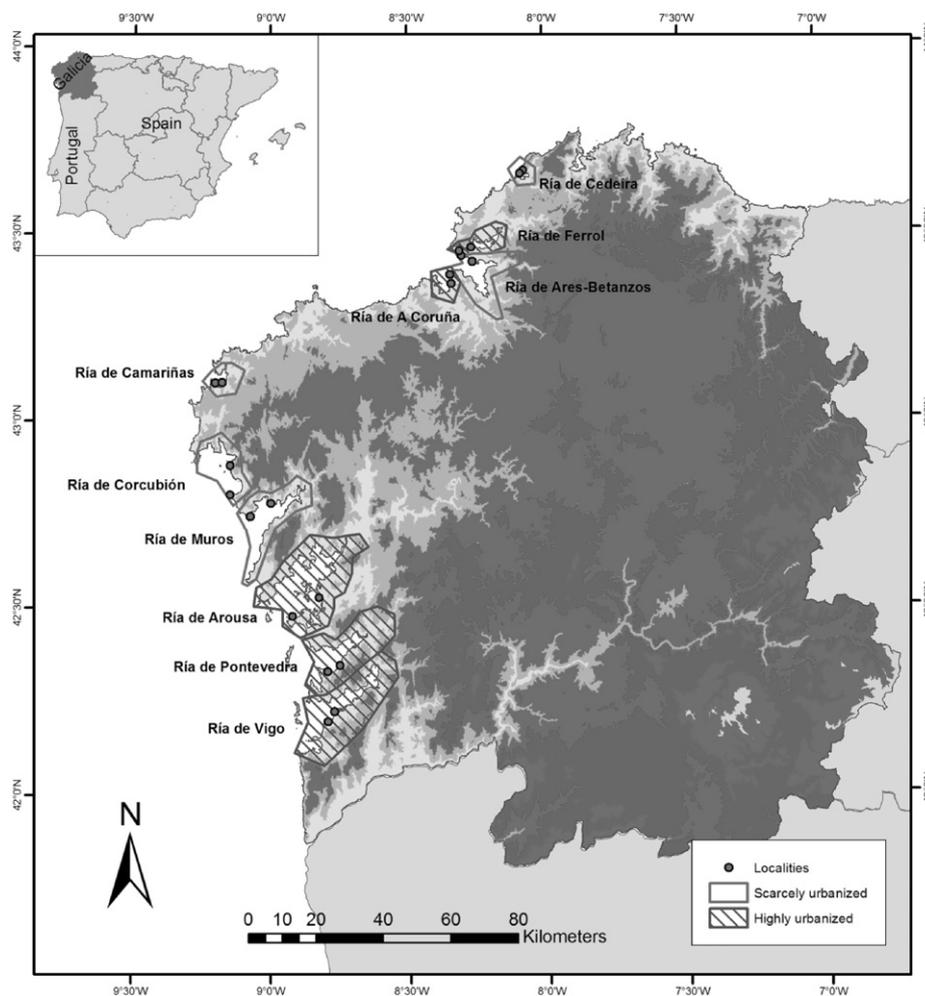


Fig. 1. Map of rias surveyed along the Galician coast showing localities within each ria. Highly and scarcely urbanized rias are also indicated.

obtained by summing over the 25 scores obtained in the sub-quadrats (Dethier et al., 1993). Macroalgae were identified to the most detailed level of taxonomic resolution achievable in the field and then aggregated into morpho-functional groups based on similarities in morphology and resource use (encrusting, foliose, leathery, filamentous and corticated algae, *sensu* Steneck and Dethier, 1994).

In those localities where *S. muticum* was present different variables such as length and number of individuals, and biomass were also quantified. In each plot, the total number of individuals and the length of at least 5 individuals of *S. muticum* selected at random, were measured. Biomass (dry-weight after drying at 60 °C for 48 h) of individuals was quantified per locality by choosing randomly 40 individuals within a 10 m² area around the sampled plots.

2.2. Data analyses

The effect of urbanization on the percentage cover, length, number of individuals and biomass of *S. muticum* was analysed using two different ANOVA models. Percentage cover, number and length of individuals of *S. muticum* were analysed using a 4-way mixed model analysis of variance including the factors: urbanization (2 levels: highly and scarcely urbanized), rias (5 levels, i.e. 5 different rias), localities (2 levels: inner and outer parts of the ria) and heights on the shore (2 levels: mid and low

shores). Urbanization (Ur) was fixed, rias (Ri) was random and nested within urbanization, localities (Lo) and heights (He) on the shore were fixed and orthogonal. Biomass was analysed using a 2-way mixed model analysis of variance. Due to the small number of individuals in some localities (e.g. Ria de Camariñas) we analysed differences in biomass among rias without taking into account the factor "Localities" neither the height on the shore. Urbanization was fixed and rias was a random factor nested within urbanization. Sixty individuals in each ria were randomly chosen for the analysis.

In order to test whether diversity of native macroalgal communities was larger in scarcely urbanized rias, the diversity of native communities (measured as number of species) was analysed following the same 4-way mixed model analysis of variance (see above).

Homogeneity of variances was examined using Cochran's test and data were transformed when necessary. Analyses of variance were followed by a *posteriori* Student–Newman–Keuls tests (SNK tests) on appropriate terms of the model found to be significant.

Different linear mixed-effects models were used to analyse the relationships between abundance of *S. muticum*, and macroalgal community diversity and level of urbanization. To test if diversity of native communities together with urbanization influenced the abundance of *S. muticum*, the percentage cover, number and length of individuals were modelled as a function of four factors (urbanization, rias, localities and heights on the shore) and number of native species as covariate. In addition, percentage cover of

S. muticum was modelled as a function of the same four factors and the different functional groups of macroalgae as covariates in order to explore the relationships between abundance of *S. muticum*, and urbanization and functional diversity. Linear mixed-effects models were implemented in R version 2.9.0. (R Development Core Team, 2005) with the lmer function (Bates and Sarkar, 2007). We used the method described by Zuur et al. (2009), with forward stepwise variables selection based on the information-theoretic approach. Random effects were fitted by the restricted maximum likelihood method (REML), and optimal fixed structures were fitted through comparisons between nested models with the same random structure using maximum likelihood (ML) estimations. We used three different families for the distributions of errors and link functions for the relationship between the mean and its linear predictor to perform the analyses. In the case of percentage cover we chose the quasibinomial distribution and the logit function, for number of individuals (count data) we chose the Poisson distribution and the log function while for length of individuals we used the Gaussian distribution and the identity function.

3. Results

3.1. Relationship between the degree of urbanization and abundance of *S. muticum*

The percentage cover, number and length of individuals of *S. muticum* did not vary significantly with the degree of urbanization. The percentage cover varied among rias, but this variation was not consistent between localities and heights on the shore (i.e. significant interaction Ri(Ur) × Lo × He, Table 1; Fig. 2a). For example, within the highly urbanized rias, the percentage cover of *S. muticum* on the low shore was greater in Ria de Vigo and Coruña than in the other rias, but only in the outer part of the rias (SNK tests, $P < 0.05$). In contrast, Ria de Arousa presented the smallest percentage cover in the inner part (SNK tests, $P < 0.05$). The number of individuals also varied significantly among rias, but inconsistently between localities (i.e. significant interaction Ri(Ur) × Lo, Table 1; Fig. 2b). For example, the number of

individuals was larger in Ria de Camariñas but only in the outer part of the ria (SNK tests, $P < 0.05$). In contrast, the length of individuals varied among rias, consistently between heights on the shore and localities (i.e. significant main effect Ri(Ur), Table 1; Fig. 2c). In this case, individuals of *S. muticum* were longer in the highly urbanized Ria de Vigo (SNK tests, $P < 0.05$, Fig. 2c).

Variation of the biomass of *S. muticum* was not related to the degree of urbanization, but it did vary significantly among rias (i.e. significant main effect Ri(Ur), $F_{8590} = 14.19$, $P < 0.001$). The biomass was greater in Ria de Ares-Betanzos, Muros and Corcubión, whereas Ria de Vigo had the greatest biomass of *S. muticum* (SNK tests, $P < 0.05$; Fig. 2d).

3.2. Role of diversity in shaping patterns of variation in *S. muticum*

The number of native species varied among rias, but this variation was not consistent between localities (i.e. significant interaction Ri(Ur) × Lo, Table 1). Only Ria de Pontevedra and Vigo had the smallest number of native species in the outer part (SNK tests, $P < 0.05$). Although marginally non-significant the number of native species tended to increase in scarcely urbanized rias, but depending on the height on the shore and locality (i.e. significant interaction Ri(Ur) × Lo × He, Table 1). There was a trend to a larger number of native species on the low shore than on the mid shore in the outer part of scarcely urbanized rias (Fig. 3).

If we analyse the significance of variables in the models, we find that only the model of the number of individuals contained significant variables (see Table 2 showing the optimal models for variables). The percentage cover and length of *S. muticum* were not affected by the number of native species as opposed to the number of individuals. In particular, the significant interaction of urbanization and number of native species in the model explaining the variability of the number of individuals (Table 2) was due to the negative relationship between the number of native species and number of individuals of *S. muticum* in highly urbanized rias, and the absence of any relationship in scarcely urbanized rias. In addition, the number of individuals was larger in highly urbanized rias than in scarcely ones. Locality (inner part vs outer part) was also a significant factor explaining variability in

Table 1
ANOVAs of the percentage cover, number and length of individuals of *S. muticum*, and number of native species. Urbanization (highly vs scarcely), localities (inner vs outer) and heights (low vs mid) were fixed and orthogonal factors and rias was a random factor nested within urbanization. Bold entries indicate significant effects of factors or interactions in the analyses.

Source of variation	df	Percentage cover		Number of inds		Length of inds		Number of native species	
		MS	F	MS	F	MS	F	MS	F
Urbanization (Ur)	1	10.69	1.07	178.60	0.26	13918.45	1.49	4.33	4.92
Rias (Ri) (Ur)	8	9.98	8.8***	693.76	3.68	9342.51	10.22***	0.88	9.43
Localities (Lo)	1	0.08	0.01	372.64	0.42	37.00	0.02	0.08	0.10
Heights (He)	1	13.45	3.97	61.60	0.87	2261.51	3.35	1.24	7.61
Ur × Lo	1	0.09	0.01	595.12	0.68	1420.83	0.79	0.27	0.33
Ur × He	1	0.15	0.04	0.01	0.01	1096.86	1.63	0.02	0.13
Lo × Ri (Ur)	8	9.40	8.29***	877.42	4.65***	1798.95	1.97	0.83	8.91***
He × Ri (Ur)	8	3.38	2.98**	70.84	0.38	674.73	0.74	0.16	1.76
Lo × He	1	0.64	0.11	226.84	3.85	908.93	0.56	0.01	0.03
Ur × Lo × He	1	3.77	0.65	102.24	1.74	1736.14	1.07	0.88	5.03*
Ri (Ur) × Lo × He	8	5.81	5.11***	58.85	0.31	1615.36	1.77	0.17	1.89 [†]
Residual	160	1.13		188.53		914.43		0.09	
Cochran's test		C=0.09 n.s.		C=0.85 $P < 0.01$		C=0.41 $P < 0.01$		C=0.10 n.s.	
Transformation		Ln (x+1)		None		None		Ln (x+1)	

Inds=individuals.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

[†] $P = 0.053$.

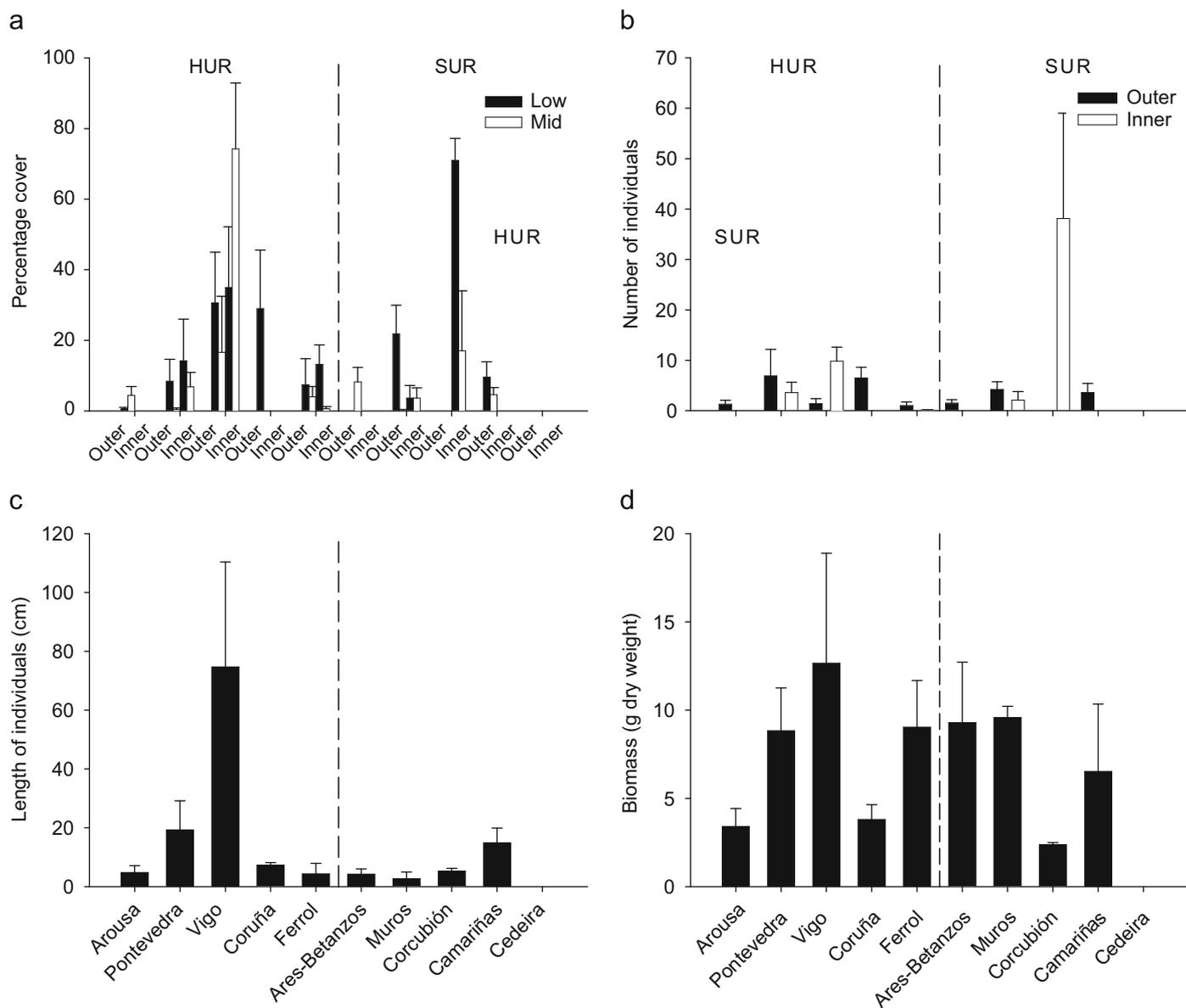


Fig. 2. Mean (\pm S.E., $n=5$) of percentage cover (a), number of individuals (0.25 m^{-2}) (b), length of individuals (c) and biomass (d) of *S. muticum* in the rias. HUR: highly urbanized rias and SUR: scarcely urbanized rias.

the number of individuals, although such a variability depended on the height on the shore (i.e. significant interaction $Lo \times He$; Table 2). It is important to highlight that the length of individuals varied significantly amongst rias as indicated by the high values of variance (418.25 ± 20.45 ; Table 2).

Functional groups of native macroalgae were not related to the percentage cover of *S. muticum*. Despite encrusting and corticated algae entered into the optimal model for explaining part of the variability of the percentage cover, they did not appear as significant variables (Table 2).

4. Discussion

This study, that included ten rias with different physical, morphological and geological characteristics (Méndez and Vilas, 2005), is the first work on the distribution of *S. muticum* carried out along the Galician coast to cover a range of 1151 km from the southern ria of Galicia, Ria de Vigo, to the northern Ria de Cedeira. This extensive survey showed that *S. muticum* was present in nine

out of ten rias, confirming its colonization in most of the intertidal rocky shores of Galicia twenty years after it was first observed in Ria de Arousa (Pérez-Cirera et al., 1989). The large expanse of *S. muticum* beds within some rias, e.g. Ria de Vigo and Ria de Pontevedra, suggests that these beds have established several years ago. *S. muticum* indeed shows high rates of spreading, although very variable, with rates from about 15 to 60 km yr^{-1} in Denmark and along the northwest American coast, respectively (Farnham et al., 1981; Stæhr et al., 2000; Lyons and Scheibling, 2009). It has been suggested that factors such as currents, prevailing winds and geography could influence its spread (Stæhr et al., 2000). Unfortunately, due to the lack of records regarding the distribution of *S. muticum* after its arrival in Galicia, it is difficult to establish a rate of spreading along this coast.

The colonization along the Galician coast is hard to explain by the reproductive mechanism of *Sargassum* in which the embryos detach from the receptacles and settle only a few meters from the parent individuals. This mechanism only facilitates short range dispersal of propagules (Kendrick and Walker, 1991). However, it is must be taken into account that gas-vesicles may enable

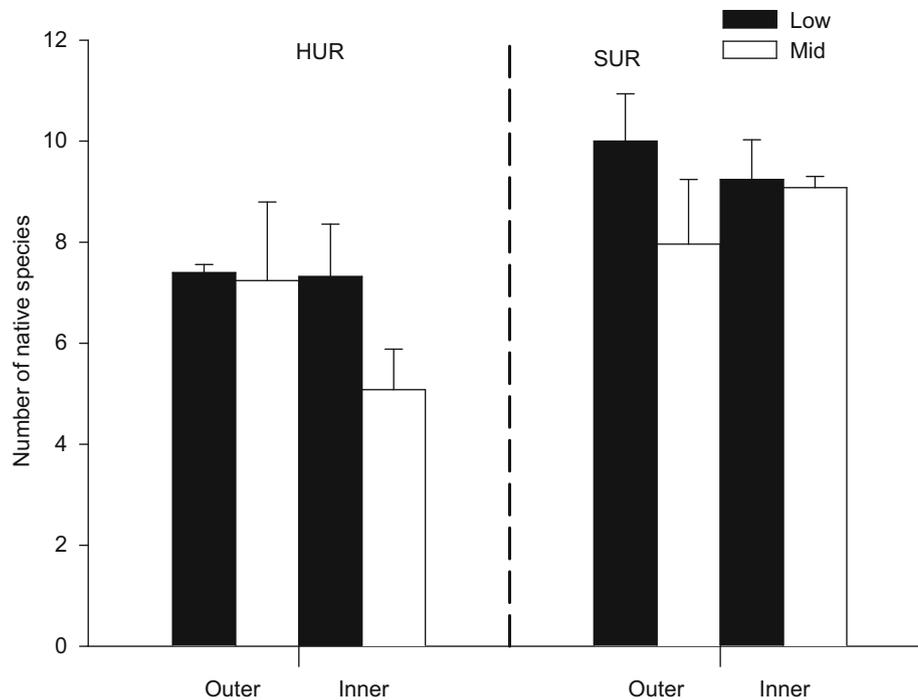


Fig. 3. Mean (+S.E., $n=5$) number of native species in the inner and outer part of highly and scarcely urbanized rias. HUR: highly urbanized rias and SUR: scarcely urbanized rias.

Table 2

Results of generalized linear mixed models for the percentage cover, number and length of individuals of *S. muticum*. Models included urbanization (highly vs scarcely), localities (inner vs outer), heights (low vs mid) as fixed factors, rias as a random factor and the number of native species and different functional groups (whenever adequate) as covariates. Bold entries denote significant effects of factors or interactions in the model. The best fitted and the full models are indicated. Abbreviations are: SE=standard error; var=variance; SD=standard deviation; AIC=Akaike's information criterion; Cort=corticated algae; Enc: encrusting algae; Fil=filamentous algae; Fol=foliose algae; and Leat=leathery algae. Abbreviations of factors are the same as in Table 1.

Response variable	Factor	Coefficients	SE	P value	var	SD	N	AIC	
Percentage cover	Encrusting	-0.03	0.02	0.19			200	80.01	
	Corticated	-0.01	0.01	0.39					
	Ri (Ur)				0.01	0.12			
Full model: Urb+Lo+He+Lo × Ur × He+Ur × He+Ur × Lo+Lo × He+Cort+Fil+Fol+Enc+Leat+Lo × Ri+He × Ri+Lo × He × Ri+Ri (Ur)									
Number of individuals	Ur	0.17	1.03	0.50			200	1239	
	Lo	-4.51	1.79	0.01					
	He	-0.98	0.80	0.22					
	Lo × He	2.88	0.36	< 0.001					
	Number of native species (NNS)	-0.003	0.01	0.80					
Length of individuals	NNS × Ur	0.15	0.03	< 0.001					
	Lo × Ri (Ur)				0.26	0.05			
	He × Ri (Ur)				0.04	0.02			
	Full model: Urb+Lo+He+Lo × Ur × He+Ur × He+Ur × Lo+Lo × He+NNS+NNS × Ur+Lo × Ri+He × Ri+Lo × He × Ri+Ri (Ur)								
	Ur	-22.01	14.36	0.26			200	1950	
Percentage cover	Lo	-6.19	6.25	0.84					
	He	6.72	4.42	0.13					
	Ur × Lo	10.66	8.84	0.23					
Length of individuals	Ri (Ur)				418.25	20.45			
	Full model: Urb+Lo+He+Lo × Ur × He+Ur × He+Ur × Lo+Lo × He+NNS+NNS × Ur+Lo × Ri+He × Ri+Lo × He × Ri+Ri (Ur)								
	Lo	-0.55	0.49	0.27			200	80.5	
Percentage cover	He	0.61	0.50	0.22					
	Ria (Ur)				0.01	0.13			
Full model: Urb+Lo+He+Lo × Ur × He+Ur × He+Ur × Lo+Lo × He+NNS+NNS × Ur+Lo × Ri+He × Ri+Lo × He × Ri+Ri (Ur)									
								169.37	

detached fronds colonize distant new locations (Deysher and Norton, 1982; Critchley et al., 1983). Thus, drifting fronds supported by buoyant vesicles may self fertilise while drifting and release viable germlings to colonize distant new locations, which seems fundamental for the colonization on large scale. Drift of fertile fronds is also considered responsible for the spread of

S. muticum from its initial point of introduction along the Pacific coast of North America (Norton, 1978), along the Scandinavian coast (Karlsson and Loo, 1999; Stæhr et al., 2000) and along the west coast of Scotland (Harries et al., 2007a). Apart from natural long distance dispersal, anthropogenic vectors for dispersal should be taken into account. Fertile individuals may be carried

for short distances entangled in anchor chains and in the steering gear of recreation and fishing boats (Kraan, 2008). This could explain, at least in part, the huge spread of *S. muticum* in the localities of the Ria de Vigo (see Fig. 2a) due to a greater traffic of fishing and recreational ships supported in this ria compared to the other ones (annual port traffic statistics of Spanish Port Systems www.puertos.es). The absence of *S. muticum* from the most northern ria surveyed, Ria de Cedeira, is difficult to explain but it might be a result of several factors related to dispersal mechanisms and lack of success in settlement and growth (Critchley et al., 1983). Specific characteristics of this ria, such as great wave exposure, reduced dimensions and geography characterized by a heterogeneous coastline and a very narrow mouth (Méndez and Vilas, 2005), could have prevented the establishment of *S. muticum*.

There was a great variability in the percentage cover, number and length of individuals at different scales, the greatest variability being found amongst localities and rias (see Table 1). This suggests that an array of both large-scale and local processes may be playing a different role in colonization and establishment of *S. muticum*. Processes that facilitate or inhibit invasion are likely to operate at different spatial scales (Stohlgren et al., 1999).

At large scale, variation in hydrodynamic conditions and topography amongst rias might influence dispersal rate of this species (see Gaylord et al., 2002; Watanabe et al., 2009). For example, great wave action and flow speeds might resuspend and flush propagules of *S. muticum* favouring dispersal over medium and long distances. Differences in topography also can affect retention rates of propagules, with slower dispersal rates in more complex rias (e.g., Ria de Cedeira) than in more open linear rias (e.g., Ria de Vigo) as suggested by Harries et al. (2007b) to explain differences in dispersal rates of *S. muticum* along the British coast. In addition, small variations in characteristics of each ria regarding temperature and salinity, productivity, availability of nutrients, wave exposure and urban disturbances might play an important role in regulating survival and growth of *Sargassum* species (Andrew and Viejo, 1998; Stæhr et al., 2000; Sánchez and Fernández, 2006; Williams and Smith, 2007). For example, nutrient enrichment enhances *S. muticum* (Sánchez and Fernández, 2006) and therefore, changes in availability of nutrients among rias could be responsible for differences in distribution of this species. Furthermore, it has been suggested that *S. muticum* is more successful in areas with high productivity (Williams and Smith, 2007). In contrast, wave exposure can restrict survival and growth of *S. muticum* (Andrew and Viejo, 1998; Stæhr et al., 2000; Harries et al., 2007b). The fact that the northern rias are more exposed and present lower levels of productivity and organic content than the southern ones (López-Jamar et al., 1992; Méndez and Vilas, 2005; Varela et al., 2005) might explain in part, differences in distribution and abundance of this species, with smaller percentage covers in the former ones. Despite urbanization has been positively related to the introduction of exotic species (Carlton, 1996), the distribution of *S. muticum* was not related to the degree of urbanization in this study. Urban disturbances that include siltation, structural modification, recreational activities or pollution, vary at different spatial and temporal scales (Mangialajo et al., 2008). Unfortunately, no data are presently available on the relative intensities of these potential urban disturbances in the rias sampled in this study. However, it is very likely that some types of disturbance or their intensities differ among rias and, consequently, their effects on the colonization/establishment of *S. muticum* might also differ. It must be also pointed out that the period and the time scale of this study (i.e. six months during the faster growth phase of *S. muticum*) might have contributed to increase magnitude differences at the scale of rias in some of the variables measured, especially the length of individuals.

At smaller scale, i.e. localities, changes in relative abundances and distributions of herbivores might affect the invasion and success of *S. muticum* (see Williams and Smith, 2007). Recent studies and on-going experimental studies with meso-herbivores from this region suggest that low grazing pressure on *S. muticum* might give the invader a competitive advantage over at least part of the native algae (Monteiro et al., 2009). In addition, changes in competitive interactions between invader and native algae, physical disturbance, habitat suitability and characteristics of recipient communities, i.e. diversity and identity of functional groups, are important local factors regulating invasion (Elton, 1958; Harries et al., 2007b; Williams and Smith, 2007). In this study, we did not find any positive or negative relationship among the percentage cover of *S. muticum* and functional groups of native algae, suggesting that mature populations of *S. muticum* are not limited or facilitated by other algae. This observation is in agreement with that of Thomsen et al. (2006) in Denmark where they did not find any relationship among abundance of *S. muticum* and other functional groups of algae. However, Deyssher and Norton (1982) and Britton-Simmons (2006) experimentally found that different native functional groups (i.e., crustose, turf and canopy algae) were important in regulating the recruitment of *S. muticum*. We suggest that different functional groups of algae might be important in early phases, i.e. recruitment or settlement, of the invasion by *S. muticum*, but less important in mature populations. Nevertheless, appropriate experiments must be done to corroborate this hypothesis.

5. Conclusions

S. muticum has successfully invaded most of the rias along the Galician coast since it was first observed in Galicia in 1986 (Pérez-Cirera et al., 1989). There was a great variability in the percentage cover, number and length of individuals at different scales, the greatest variability being found among localities and rias. This suggests that an array of both large-scale and local processes may play a different role in colonization and establishment of *S. muticum*.

Because of their worldwide distribution and ability to alter native communities (Williams and Smith, 2007), introduced algae are potentially important agents of global ecological change. This study illustrates the presence and distribution of an introduced alga in a large area. These results, in combination with recent studies (e.g. Britton-Simmons and Abbott, 2008; Engelen and Santos, 2009) and on-going experiments on the effects of *S. muticum* along the Galician coast (e.g. Incera et al., 2009; Olabarria et al., 2009a, b; Rossi et al., 2010) highlight the importance of future research into the distribution and impact of introduced algae and prove the urgent need for monitoring programmes and increasing efforts to prevent and control new introductions.

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