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ORIGINAL PAPER

Macro- and mesoherbivores prefer native seaweeds over the invasive brown seaweed *Sargassum muticum*: a potential regulating role on invasions

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Abstract Herbivory has a strong impact on algal distribution, abundance and community structure and may influence the establishment and spread of introduced seaweed species. In this study, we assess the potential regulating role of herbivory on one of the most invasive brown seaweeds: *Sargassum muticum*. Multiple choice feeding experiments were conducted with 13 native seaweeds, *S. muticum* and 5 herbivore species from the Northwest, Southwest and South of Portugal. *S. muticum* was always the least or among the least preferred seaweeds and attained one of the highest growth rates of the tested seaweeds, with and without herbivores. The addition of herbivores increased the number of cases by 40% in which the invader had higher growth rates. Our results suggest that low grazing pressure on *S. muticum* by the recipient herbivore community may give the invader a competitive advantage over at least part of the native seaweed community, thereby contributing to the invasiveness of *S. muticum* along the Portuguese coast.

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Introduction

Species invasions threaten the integrity of natural ecosystems and annually cause billions of dollars of economic losses worldwide (Mack et al. 2000). Human activity, by providing the required dispersal vectors and increasing the susceptibility of natural communities, has a pronounced influence on the number of introductions and consequently on the number of successful invasions. Biological invasions are a global problem. Because introduced species can cause such harm, and because the processes by which introduced species succeed address fundamental ecological theory, much recent attention has been devoted to understanding invasion biology (Mack et al. 2000; Torchin and Mitchell 2004).

The success of non-indigenous species is dependent on a complex combination of (1) intrinsic characteristics of non-indigenous species (see Engelen and Santos 2009), which often have broad ecological requirements and tolerance (e.g. large geographical range), r-selected life histories (Baker 1974), association with disturbed or anthropogenic habitats (Sakai et al. 2001) in combination with propagule pressure (Britton-Simmons and Abbott 2008) and origins from large continents with diverse biotas and (2) characteristics of recipient ecosystems, in particular, the biological environment, e.g. the absence of predators, herbivores, parasites and diseases (for references see Sax and Brown 2000).

Herbivory plays an important role in seaweed distribution, abundance and community structure (Duffy and Hay 2000) and could be an important factor in seaweed invasions. It is frequently considered that a reduced predation is a great advantage for non-indigenous species in comparison with native species (Mitchell and Power 2003) and that this would increase the success and spread of non-indigenous species (Wilson 1989). Some invasion theories stress the importance of grazing or rather the lack of grazing on invasive species relative to native species. The Enemy Release Hypothesis (ERH) is based on the assumptions that the specialist enemies of the invasive species are absent in the invader region and/or the native enemy species are slow to include the introduced species in their diets. This theory is supported by studies performed with terrestrial plant invaders (see Mack et al. 2000; Mitchell and Power 2003; Torchin et al. 2003), but especially in the recent years has been criticised by authors that found evidence against this theory (Parker and Hay 2005; Parker et al. 2006). However, few studies have been performed to test the interaction between invader seaweeds and herbivores in their introduced range (but see Vermeij et al. 2009) testing the assumption that enemies exert top-down control on the invader in its native region. Most studies have focused on the influence of competitor removal on the establishment of invading seaweeds (e.g. Valentine and Johnson 2003).

In temperate subtidal and intertidal communities, the important herbivores are molluscs (e.g. gastropods), sea urchins (Hawkins and Hartnoll 1983) and fishes (e.g. Vergés et al. 2009). Gastropod grazing is thought to be the most important factor determining the upper limit of lower algal beds (Jernakoff 1983). Sea urchin grazing, on the other hand, has been reported to play an important role in regulating the distribution, abundance and diversity of native macroalgae in subtidal communities (Lawrence 1975). Sea urchins are able to decimate temperate kelp beds (Lawrence 1975; Steinberg et al. 1995), and can influence the establishment, spread and persistence of introduced algal species (Baltz and Moyle 1993; Sumi and Scheibling 2005). Many studies have focused on the importance of sea urchins and fishes in regulating macroalgae. Few studies on smaller herbivores, such as amphipods, polychaetes, isopods, small crabs, shrimps and gastropods have been done (Cruz-Rivera and Hay 2000), but their impacts on plant community can be important when they are dominant (Brawley 1992; Duffy and Hay 2000). Mesograzers feed on host seaweeds and their epibionts and constitute important prey for many fish species (Edgar and Shaw 1995a, b) providing an important link between primary producers and large predators in littoral food chains (Wikström 2004).

Not all parts of seaweed are equally consummated by herbivores because they differ in nutrition, toughness or chemical defence levels (Cronin 2001). According to the optimal defence theory (ODT; Cronin 2001), tissues that are more essential to the survival of the individual or its species would be less palatable (Cronin 2001), basal and reproductive parts, for example, would be tougher and/or better chemically defended than young photosynthetic tissue.

The aim of this study was to compare the preference of native herbivores for native seaweeds versus the introduced seaweed *S. muticum*. Representative seaweeds and herbivores from several seaweed communities along the Portuguese coast were used. In addition, we tested the food preference of three herbivores between vegetative and reproductive tissue of some reproductive seaweeds from one of the regions. According to the ERH and the ODT, we should expect that herbivores show a lower preference both for the introduced seaweed and for the reproductive tissue.

Materials and methods

Study organisms and sites

The model invader of this study is the Asian brown seaweed *Sargassum muticum* (Yendo) Fensholt 1955 a pest species that can form dense beds and can reduce the abundance of native seaweeds and possibly seagrasses (Ambrose and Nelson 1982; Critchley et al. 1986; Britton-Simmons 2004; Tweedley et al. 2008). Japanese oyster (*Crassostrea gigas*) imported from Japan (Critchley and Dijkema 1984) was probably the primary vector for the introduction and subsequent spread of *S. muticum* within European waters (Critchley and Dijkema 1984) as well as along the west coast of North America in the late 1940s (Ambrose and Nelson 1982). In Europe, this species was found for the first time in 1973 at Bembridge, Isle of Wight, England (Farnham et al. 1973) and presently is distributed from Norway to Portugal (Engelen and Santos 2009).

Experiments were conducted with seaweeds and grazers from three regions in Portugal: the Northwest Atlantic represented by Praia Norte in Viana do Castelo, the Southwest Atlantic represented by Praia Queimado, Porto Covo and the South Atlantic represented by Ria Formosa, Faro.

Northwest Portugal species

In Praia Norte (41°41′47N, 8°51′14W), Viana do Castelo, the invasive *S. muticum* has a wide vertical distribution from mid-intertidal pools to the shallow subtidal. The shallow subtidal and low-intertidal channels are dominated by *S. muticum*, *Chondrus crispus*, *Osmundea osmunda* and *Mastocarpus stellatus*. The low-intertidal pools are dominated by *S. muticum*, *Bifurcaria bifurcata* and *Laminaria ochroleuca*. Therefore, these native seaweeds were selected for the feeding experiments together with the four dominant herbivore species: (1) the gastropods *Gibbula umbilicalis* and *Gibbula pennanti* that inhabit the mid- and low-intertidal and are commonly found under the branches of *S. muticum*; (2) the sea hare *Aplysia punctata* that inhabits the low-intertidal and subtidal zones and (3) the sea urchin *Paracentrotus lividus* that inhabits the low-intertidal and subtidal in Viana do Castelo.

Gibbula umbilicalis and *G. pennanti* are eastern Atlantic species, which are abundant on rocky shores in Portugal, at low and mid-levels of the intertidal zone where wave energy is low (Gaudèncio and Guerra 1986). They are found in mixed populations and favour rocky platforms with a dense algal cover, but may also be found in pools, under stones and on the upper surfaces of boulders. Densities of 130–200/m^2 are general and may occasionally approach 300 (Gaudèncio and Guerra 1986). *P. lividus* (Lamarck) is one of the most important invertebrate seaweed herbivore in the Mediterranean Sea (Boudouresque and Verlaque 2001; Palacín et al. 1998) with densities locally reaching 10–30 individuals per square metre in shallow, hard substrate (e.g. Benedetti-Cecchi and Cinelli 1995; Sala et al. 1998). This species was also selected because it is documented as a generalist herbivore with a key role function in regulating the distribution, abundance and diversity of native macroalgae (Lawrence 1975) and have been reported to reduced the abundance of *S. muticum* in the Mediterranean Sea (Ribera and Boudouresque 1995). It is expected that these species play a role in the local *S. muticum* invasion. *Aplysia punctata* has been described to consume *S. muticum* (Critchley et al. 1986), and the sea urchins have been recognised as important players on the establishment, spread and persistence of introduced algal species (e.g. Baltz and Moyle 1993; Sumi and Scheibling 2005). The multiple choice feeding experiments lasted 3, 9 and 1 day for *Gibbula* spp., *A. punctata* and *P. lividus*, respectively. In addition, we performed food preference experiments comparing reproductive and vegetative tissue of the seaweeds *M. stellatus*, *C. crispus* and *S. muticum*, with *A. punctata* and *Gibbula* ssp. during 2 and 9 days, respectively.

Southwest Portugal species

In Praia do Queimado (37°49′36N, 8°47′32W), Porto Covo, *S. muticum* is restricted to sheltered intertidal pools which are mostly dominated by *Cystoseira humilis* (Engelen et al. 2008; Engelen and Santos 2009), but also contain *Sargassum vulgare*, *Dictyota dichotoma*, *Cladostephus spongiosus*, *Stypocaulon scoparium* and *Dictyopteris polypodioides*. All these species were selected for the feeding experiments. The grazers were represented by the amphipod *Gammarus insensibilis*, one of the most common groups of mesograzers in temperate marine environments with densities often reaching several thousand individuals per square metre (Brawley 1992) and the gastropod *Hydrobia ulvae* that is commonly found on macroalgae such as *Stypocaulon scoparium*, *Ulva*, *Enteromorpha* and fucoids (Barnes and Greenwood 1978; Barnes 1979). *Hydrobia ulvae* may feed mainly on silt, epiphytic diatoms and green seaweeds rather than on most macroalgae themselves (Fish and Fish 1996). Abundance of *Hydrobia* spp. vary strongly with season and locations, e.g. from 440 + 260 individuals per square metre in June 1996 to 35,520–14,544 individuals per square metre in August 1996 (Schories et al. 2000). The feeding experiments with each species lasted 7 days.

South Portugal species

In the Ria Formosa lagoon, *S. muticum* has established around 2002 on the lagoon side of the sand bar Ilha Deserta (36°58′29N, 7°56′24W) and can be found in the subtidal together with the seaweeds *Gracilaria multipartita*, *Gracilaria longissima* and *Codium decorticatum*. The native *S. vulgare* was added to the selected native seaweeds as this is one of the few *Sargassum* species that has an overlapping distribution with *S. muticum* in the south of Portugal. The sea urchin *P. lividus* was used as a macrograzer in the multiple choice feeding experiment that lasted 2 days.

Design of multiple choice feeding experiments

After collection and before the feeding experiments, herbivores were kept on a diet of seaweeds among which they were collected. We explicitly did not use a pre-experiment food-deprivation period. To test the herbivores' food preference, we performed multiple choice feeding experiments with combinations of *S. muticum* and the selected native seaweeds and herbivores. The effect of each herbivore species within a specific region was assessed in a separate experiment. For each herbivore treatment, we used either five individuals of *G. insensibilis*, or 20 individuals of *H. ulvae*, or 8 individuals of *Gibbula* spp., or 2 juvenile individuals of *A. punctata*, or 1 adult individual of *P. lividus*. These numbers were established based on a combination of the size of the animals relative to the size of the experimental unit as not to cause unnatural behaviour, their natural densities per surface area and the amount of seaweed biomass that could be placed in each unit. Most combinations probably reflect the natural situation reasonably, with the exception of *P. lividus,* which is usually encountered in higher density patches that are almost free of any canopy forming seaweeds. The *A. punctata* individuals of a few centimetres that were used would most probably in the field have been foraging in a larger area than available in the experimental unit.

Previous to each experiment all seaweed tissues were cleaned by hand of all macroscopic fouling organisms, cut into pieces of similar weights of ~2 gWW and acclimated to the laboratory conditions for 2 days. We expect that the acclimation period prevented differences in palatability between seaweed species due to induced chemical defences as a reaction to grazing histories (Weidner et al. 2004) or to the cutting (Rohde et al. 2004). The size of each seaweed piece was standardised for each experiment. Tissue pieces were blotted and weighed to the nearest milligram. A mixed seaweed diet was delivered to herbivores in individual aquaria of 2 l capacity (12 replicates, dimensions 12 cm × 18 cm × 11 cm) of an open flow-through system provided with natural seawater (32 promille salinity, [N] <5 mM) and 12:12 L:D regime and with light levels around 1,210 lux (PeakTech lightmeter 5025) provided by a 58 Watt Osram 55 colour 10 lamp. Flow rates (200 ml min^{-1}) were assumed sufficient to prevent nitrogen limitation in control units and elevated nitrogen levels in treatment units because of faecal pellets. Autogenic changes (Peterson and Renaud 1989) were controlled with 12 replicate aquaria without herbivores. All treatment and control replicates were maintained under the same experimental conditions and were run at the same time. Each of the experiments was ended entirely as soon as one of the tissues in one of the replicates was estimated to reach 50% consumption, then, herbivores were removed, and all algae tissue was blotted and weighed.

Statistical analysis

The biomass consumed was calculated using the equation [(Ho × Cf/Co) − Hf], where Ho and Hf are the initial and final wet weights of algae, respectively, and Co and Cf are the initial and final weights of the control, respectively (Sotka et al. 2002). Growth rates were calculated as the difference between the initial and final wet weights relative to the initial wet weight divided by the number of days. Since the data of each seaweed obtained within an experimental unit cannot be assumed to be independent, classical ANOVA is inappropriate (Roa 1992), and a permutation test was used instead to analyse growth and consumption of seaweeds. To assess differences in growth rates among seaweeds and herbivore feeding preferences among food types, multiple choice experiments were analysed by permutation tests (Rohde et al. 2004; Bärlocher 2005; Yun et al. 2007; Abelho and Molles 2009). The assumption of exchangeability required for a permutation test was assured by random allocation of treatments to the experimental units and heterogeneity of variances was tested using Cochran's test, in all cases variances were homogeneous indicated by $P > 0.05$ of the Cochran's test (Underwood 1997). In short, the permutation tests were performed as following for the consumption data: we first tabulated the consumption data of each individual herbivore for each food type. We then calculated differences in consumption between all possible pairs of food types and values were then shuffled. To determine whether consumption for pairs of food items was significantly different, the mean real differences in consumption between two food types were compared with the shuffled values (run 10,000 times; equivalent of randomly assign measured consumption values to the available food items). The probability differences being due to chance (proportion of differences in consumption values obtained by reshuffling as large as the original values) were given by the number of times the real difference was higher than the random assigned difference, divided by the number of runs (10,000) with $\alpha = 0.05$.

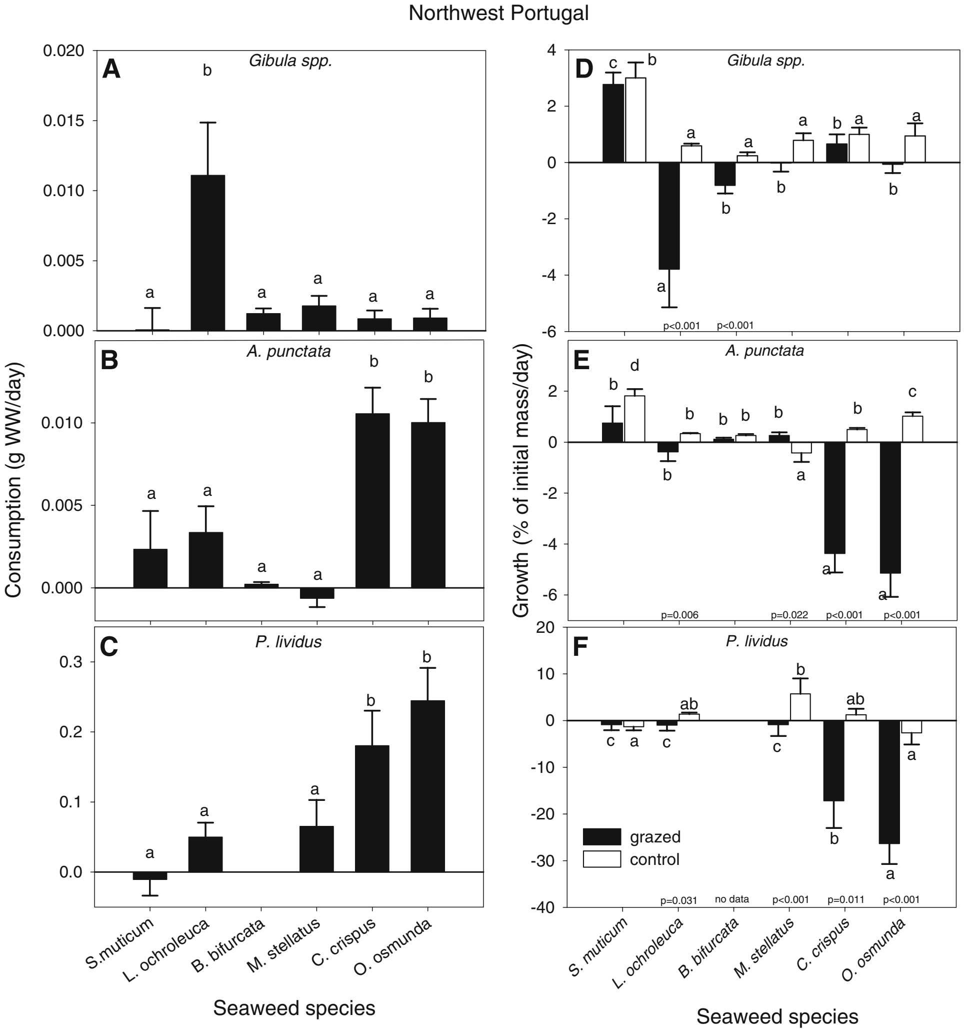
Results

Northwest Portugal species

The gastropod *Gibbula* spp. showed a strong preference for *L. ochroleuca*, consuming six times more *L. ochroleuca* than the other seaweeds ($P < 0.0001$), including *S. muticum*, which was the least consumed (Fig. 1a). The seaweeds *L. ochroleuca* ($P < 0.001$) and *B. bifurcata* ($P < 0.001$) were significantly grazed (Fig. 1d). Both with and without the presence of *Gibbula* spp., the highest relative net growth rates were accomplished by *S. muticum* (Fig. 1d). Growth rates among the native seaweeds did not differ when the herbivore was absent (Fig. 1d). In contrast, *A. punctata* and *P. lividus* showed a clear preference for *O. osmunda* ($P \leq 0.0001$ and $P \leq 0.003$, respectively) and *C. crispus* ($P \leq 0.002$ and $P \leq 0.0047$, respectively) over the other seaweeds, including *S. muticum* (Fig. 1b, c). *A. punctata* significantly affected the net growth of *S. muticum*, *B. bifurcata*, *M. stellatus* and *C. crispus* (Fig. 1e), whereas *P. lividus* affected the growth of all the native seaweeds, except *S. muticum* (Fig. 1f). In all control treatments (no grazing), *S. muticum* attained the or one of the highest relative growth rates (Fig. 1e, f), and most native seaweeds showed very similar relative growth rates among each other (Fig. 1e, f). In the grazing treatment, *S. muticum* also had among the highest net growth rates.

Gibbula spp. clearly preferred the reproductive tissue more than the vegetative tissue in *S. muticum* and *M. stellatus*, but the consumption was significantly more in *S. muticum* and *M. stellatus* over *C. crispus* that was consummated intermediately (Fig. 2a). The reproductive tissues of all seaweeds and the vegetative tissue of *C. crispus* were grazed upon (Fig. 2c). The vegetative tissue of *S. muticum* had the highest relative (net) growth rates with and without the presence of the gastropods. However, the reproductive tissue of *S. muticum* had (one of) the lowest relative growth rates in the treatment with(out) the gastropods (Fig. 2c). *Aplysia punctata*, on the other hand, had a clear preference for *C. crispus* reproductive tissue over both the reproductive and vegetative tissues of the other seaweeds ($P \leq 0.0001$; Fig. 2b). The vegetative tissue of *S. muticum* had the highest growth rates without the grazer and was among the fastest net growers in the presence of *A. punctata* (Fig. 2d).

Fig. 1 Mean consumption (gWW) by the mesoherbivores *Gibbula* spp. (**a**), *Aplysia punctata* (**b**) and *Paracentrotus lividus* (**c**) of the introduced species *Sargassum muticum* and the native seaweeds *Laminaria ochroleuca*, *Bifurcaria bifurcata*, *Mastocarpus stellatus*, *Chondrus crispus* and *Osmundea osmunda* from Northwest Portugal. Net growth of these seaweeds with (*black bars*) and without (*open bars*) *Gibbula* spp. (**d**), *A. punctata* (**e**) and *P. lividus* (**f**) from multiple choice feeding experiments. *Bars* indicate standard error ($n = 12$); *lower case letters* indicate grouping of means (means which have one or more letter in common are not significantly different at $P = 0.05$. *ND* indicates the absence of *B. bifurcata* in the experiment with *P. lividus*



Southwest Portugal species

The two herbivores tested showed different consumption patterns. The amphipod *G. insensibilis* showed a clear and very strong food preference for *S. scoparium* ($P \leq 0.0001$), relative to the other seaweed species, including *S. muticum* ($P \leq 0.0001$), which were all slightly consumed (Fig. 3a). In the control treatment (no grazing), the native seaweeds *D. dichotoma* and *C. humilis* showed the highest, *S. muticum* and the native seaweeds *S. vulgare*, *S. scoparium* and *D. polypodioides* showed intermediate and *C. spongiosus* the lowest relative growth rate(s) (Fig. 3c). With the presence of the amphipod *G. insensibilis* , the lowest relative net growth rate was recorded for the heavily grazed *S. scoparium*; all the other seaweeds inclusive *S. muticum* showed very similar relative net growth rates (Fig. 3c). None of the seaweed species was consumed significantly by the gastropod *H. ulvae* ($P \geq 0.0832$; Fig. 3b, d). However, there were some differences in the relative growth rates among the different seaweed species within each treatment, which were very similar with and without *H. ulvae*. The seaweeds *D. dichotoma* and *C. humilis* attained the highest relative growth rate, followed by *S. scoparium* and the seaweeds *S. muticum*, *S. vulgare* and *D. polypodioides* with intermediate growth rates and *C. spongiosus* had the lowest growth rate (Fig. 3d).

South Portugal species

The sea urchin *P. lividus* clearly preferred to feed on *G. longissima* ($P \leq 0.0003$), consuming 3–5 times more this than the other species (Fig. 4a). *S. muticum* was among the least consumed seaweed species. All seaweed species, except *C. decorticatum*, were grazed upon by *P. lividus* (Fig. 4b). In the absence of *P. lividus*, the seaweeds *C. decorticatum* and *G. multipartita* had higher relative growth rates than *S. muticum* and *S. vulgare* (*P* values ranging from 0.0061 to 0.0229). *G. longissima* had intermediate growth rates (Fig. 4b). With the presence of *P. lividus*, the seaweeds *S. muticum*, *C. decorticatum* and *G. multipartita* had

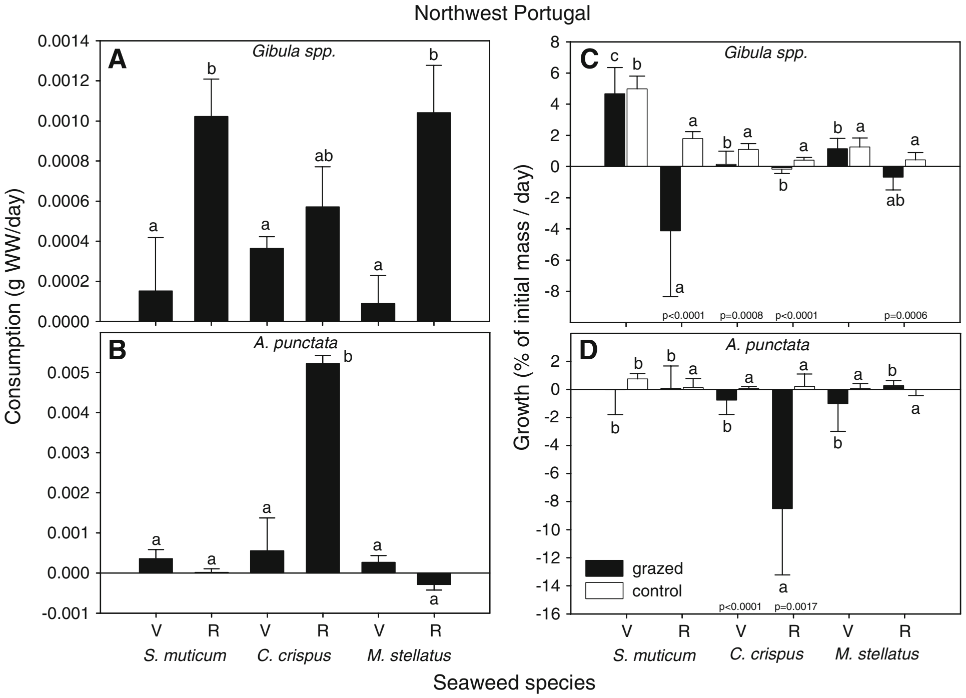


Fig. 2 Mean consumption (gWW) by the mesoherbivores *Gibbula* spp. (**a**) and *Aplysia punctata* (**b**) of vegetative (represented by *V*) and reproductive (represented by *R*) tissue of the introduced species *Sargassum muticum* and the native seaweeds *Chondrus crispus* and *Mastocarpus stellatus* from Northwest Portugal. Net growth of these seaweeds with (*black bars*) and without (*open bars*) *Gibbula* spp. (**c**) and *A. punctata* (**d**) from multiple choice feeding experiments. *Bars* indicate standard error ($n = 12$); *lower case letters* indicate grouping of (treatment) means (means which have one or more letter in common are not significantly different at $P = 0.05$); *P* values printed show significant differences ($\alpha = 0.05$) between treatments within the seaweed species indicated

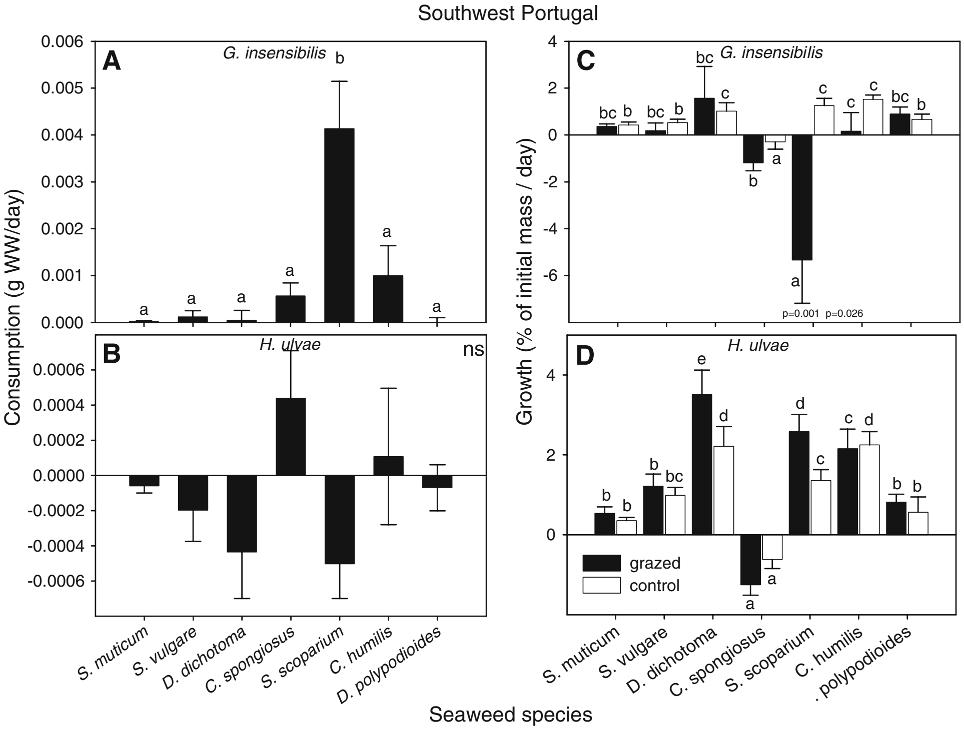


Fig. 3 Mean consumption (gWW) by the mesoherbivores *Gammarus insensibilis* (**a**), *Hydrobia ulvae* (**b**) of the native seaweeds *Sargassum vulgare*, *Dictyota dichotoma*, *Cladostephus spongiosus*, *Stypocaulon scoparium*, *Cystoseira humilis* and *Dictyopteris polypodioides* and the introduced species *Sargassum muticum* from Southwest Portugal. Net growth of these seaweeds with (*black bars*) and without (*open bars*) *G. insensibilis* (**c**) and *H. ulvae* (**d**) from multiple choice feeding experiments. *Bars* indicate standard error ($n = 12$); *lower case letters* indicate grouping of (treatment) means (means which have one or more letter in common are not significantly different at $P = 0.05$); *NS* = no significant differences detected ($\alpha = 0.05$); *P* values printed show significant differences ($\alpha = 0.05$) between treatments within the seaweed species indicated

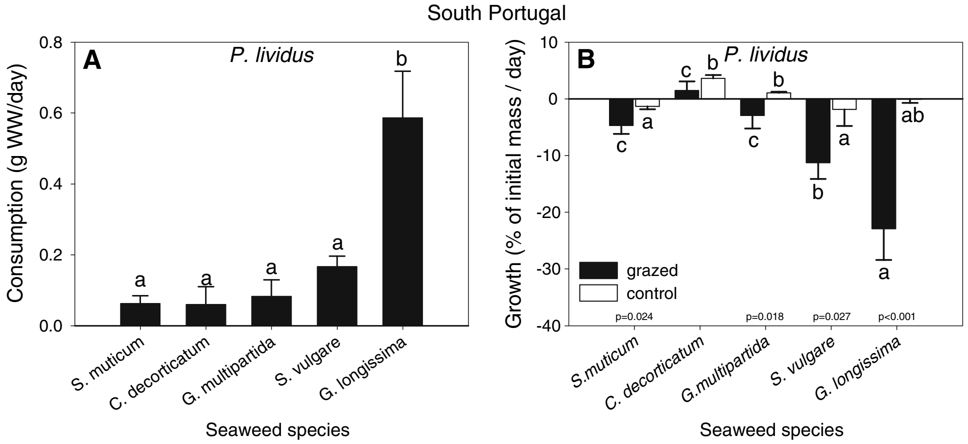


Fig. 4 Mean consumption (gWW) by the sea urchin *Paracentrotus lividus* of the native seaweeds *Gracilaria multipartita*, *Gracilaria longissima* and *Codium decorticatum* and the introduced species *Sargassum muticum* from South Portugal (**a**) and net growth of these seaweeds with (*black bars*) and without (*open bars*) *P. lividus* (**b**) from multiple choice feeding experiments. *Bars* indicate standard error ($n = 12$); *lower case letters* indicate grouping of (treatment) means (means which have one or more letter in common are not significantly different at $P = 0.05$); *P* values printed show significant differences ($\alpha = 0.05$) between treatments within the seaweed species indicated

relative net growth rates higher than *S. vulgare* (*P* values ranging from 0.0067 to 0.0273) and *G. longissima* (all *P* values < 0.0001).

Discussion

Our results show that macro- and mesoherbivores from the Portuguese coast prefer many native seaweeds over the introduced seaweed *Sargassum muticum*. In all but one food preference experiments, *S. muticum* was the least or among the least preferred seaweeds. We did not detect any regional differences in the low preference of herbivores for *S. muticum,* despite the fact that regions differ strongly in the time since colonisation, as the species arrived about 22, 12 and 7 years ago in Northwest, Southwest and South Portugal (Engelen unpublished data). Previous studies have also suggested low food preferences of native herbivores for invasive *S. muticum* e.g. the sea urchins *A. punctuate* (Critchley et al. 1986) and *Strongylocentrotus droebachiensis* (Britton-Simmons 2004). The same was observed for other invasive seaweeds (Schaffelke et al. 1995; Wikström et al. 2006) and terrestrial plant invaders (Colautti et al. 2004). Only in the case of the sea urchin, *Psammechinus miliaris* in Denmark a weak feeding preference for *S. muticum* over the native *Halidrys siliquosa* was observed (Pedersen et al. 2005). The palatability of tissues/species are due to differences in nutritional content or in the chemical components associated with defence (van Alstyne et al. 1999). The low grazing observed in this and other studies with *S. muticum* could be linked to the presence of secondary metabolites as indicated by the presence of relatively high levels of phenolic compounds in the genus *Sargassum* (Gorham and Lewey 1984; Hay and Fenical 1988; Connan et al. 2006). These compounds are considered to be the main defences against herbivores although theses substances may have a variety of other functions (Hay and Fenical 1988, and for further review see Jormalainen et al. 2001). In general, some seaweed tissues are less protected than others and as a consequence preferred by herbivores. Reproductive tissues are more protected than vegetative parts as indicated by their higher phenolic content in, e.g. *Alaria marginata* (Steinberg 1984) and *Fucus vesiculosus* (Tuomi et al. 1989). However, the contrary has also been reported in *Ascophyllum nodosum* (Pavia et al. 2002), in which, *Gibbula* spp. and *A. punctata* clearly preferred reproductive over vegetative tissue. Many small and relatively sedentary herbivores such as amphipods, polychaetes and crabs, may preferentially feed on defended seaweeds and tissues in order to minimize their susceptibility to natural enemies (Holmlund et al. 1990; Duffy and Hay 1994).

This will reduce their reproductive success thus their competition and ability competition among seaweeds within a community (see Vergés et al. 2007 and references therein). However, fertility of invaders may have a low contribution to population growth rate as demonstrated for the brown seaweeds, *Ascophyllum nodosum* (Pavia et al. 2002) and *S. muticum* (Engelen and Santos 2009) and red seaweeds like *Gracilaria gracilis* (Engel et al. 2001).

In our experiments, independent of the region of origin, the more mobile herbivores had a food preference for specific red seaweeds. The sea hare *A. punctata*, for example, showed a clear consumption preference for the red algae *C. crispus* and *O. osmunda*, but not *M. stellatus*, whereas the sea urchin *P. lividus* preferred the red algae *C. crispus* and *O. osmunda* and *G. longissima* (but not *G. multipartita*).

However, less mobile species such as the gastropods *Gibula* spp. and the amphipod *G. insensibilis* preferred brown seaweeds as food, feeding almost exclusively on *L. ochroleuca* and *S. scoparium*, respectively. Marine herbivores are primarily generalist feeders (Lubchenco and Gaines 1981; Steneck 1982; Hay and Fenical 1988). Larger herbivores such as fishes, sea urchins and some gastropods are generalized feeders (for further review see Hay 1992), since they are very mobile and may move among and feed from thousands of plants each day. They use seaweeds as food rather than living sites (Hay 1992). Diet-specificity may be associated with small herbivore size and short herbivore life span (Lubchenco and Gaines 1981; Steneck 1982; Hay et al. 1987; Hay and Fenical 1988). Specificity in marine invertebrates may also be correlated with feeding mode. Only a few species of scraping herbivores are known to be specialists (e.g. some chitons and limpets: Morris et al. 1980; Steneck 1982). Furthermore, while many of the chewing herbivores (e.g. some isopods, cranefly larvae, chironomid larvae and sea hares) are associated with one or a few plant species (Morris et al. 1980), only sea hares have been shown to be oligophagous (Carefoot 1987). However, any kind of categorising is difficult as closely related consumers can sometimes exploit quite different food sources (Paul et al. 2001). Of importance might also be that red and brown seaweeds differ in their secondary metabolites (for further review see Amsler and Fairhead 2006).

Co-occurring mesograzers species can have different feeding preferences (this study, Duffy and Hay 2000 and references therein). These differences in feeding preference can have important consequences for community organization (Duffy and Hay 2000). The food preference of most herbivore species used in this study agree with previous studies that, for example, juvenile sea hares have restricted diets (i.e. feeding specialist), usually limited to one or few types of algae (Pennings 1990) and prefer a diet of a chemical rich red algae (Carefoot 1987). On the other hand, we observed that the sea urchin *P. lividus* clearly preferred some red species even though it can be considered a generalist on the studies of some (Lemée et al. 1996), others have shown clear food preferences of this species for some seaweeds, like kelp (Scheibling and Antony 2001; Sumi and Scheibling 2005). The amphipod *G. insensibilis*, considered to be a green seaweed food specialists, commonly associated with *Chaetomorpha linum* (Sheader and Sheader 1985) in the absence of green algae as in our experiments, consumed almost exclusively the brown seaweeds *S. scoparium*. Our study and several others (e.g. Rogers et al. 2003) suggest that categorising herbivores as generalists or specialists is not always straight forward as species are not always specialist or generalist per se. A generalist might be able to consume many species, but this does not mean that it does not prefer some to others. On the other hand, a specialist is not able to consume alternative food source to the preferred species. The multiple choice feeding preferences of the different herbivores investigated form a complex pattern of food choice. Clearly some seaweeds that seem very similar and are closely related, like *M. stellatus* and *C. crispus*, are very different for some of the herbivores leading to contrasting food choices for example between the used seahare and the seaurchin. Only an array of studies combining the nutritional values, defensive compounds in combination with vital rates of the herbivores can elucidate the choices made by herbivores and contribute to an explanatory model that predicts who eats what. However, food preference of marine herbivores under field conditions may become uncoupled with the specific biochemical value of food as a result of the effects of seaweed morphology, chemical defences and habitat refugia (Barile et al. 2004 and references therein) complicating the translation of laboratory experiments to field conditions.

We are unaware of any experimental study that examined top-down control of the seaweed species/communities used in this study; however, top-down control of seaweeds is common in non-eutrophicated areas (e.g. Lotze et al. 2001; Diaz-Pulido and McCook 2003; Boaventura et al. 2002) as most of the coast of Portugal is, especially in the intertidal (Lubchenco and Gaines 1981; Paine 2002). For most late successional brown seaweeds, as used in this study, this control acts probably more strongly on recruits rather than larger individuals (e.g. Diaz-Pulido and McCook 2003).

One of the most cited invasion theories, the ERH, states that introduced species can become invasive because they have gained a competitive advantage over native species in the recipient region due to the absence of natural enemies (Maron and Vilà 2001; Keane and Crawley 2002; Siemann and Rogers 2003). Herbivores in the recipient region are assumed to prefer native over the invasive food source, which should lead to a competitive advantage of the invader of the native species. This advantage can be expressed in many traits, but some like growth rate, size and reproductive output could be of major importance for the success of invaders. Our results suggest that the meso-herbivores that are native to the Portuguese coast prefer (certain) native seaweeds over the invasive seaweed *S. muticum*. Furthermore, when relative growth rate is considered as an indicator trade the grazing preference of native herbivores can give the invasive seaweed *S. muticum* a competitive advantage over various different native seaweeds of the Portuguese coast. However, the ERH can only be properly tested when including additional information on the intensity of predation experienced by an invasive species in its native range (Vermeij et al. 2009).

The introduction, spread and proliferation of invasive seaweeds, like *S. muticum*, are linked to human activities that provide dispersal vectors (e.g. shipping and aquaculture) and disturbances (e.g. habitat degradation and biodiversity loss) that facilitate establishment (reviewed in Williams and Smith 2007). Besides these factors, specific characteristics of *S. muticum*, like high growth rates (Pedersen et al. 2005, Engelen unpublished data), high reproductive output (Umezaki 1984) and high dispersal capacity (Critchley and Dijkema 1984) are considered to promote invasiveness, although locally persistence of adults seems to contribute most strongly to population growth (Engelen and Santos 2009). We conclude that, in addition to the above-mentioned factors, the low feeding preference for *S. muticum* by herbivores in recipient seaweed communities in Portugal may facilitate invasions as growth rate differences between the invader and many native seaweeds were affected by grazing in the advantage of the invader.

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