

A REVIEW OF HERBIVORE EFFECTS ON SEAWEED INVASIONS

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Almost 300 non-native seaweeds are identified worldwide and an increasing number of these are classified as invasive with potential negative effects on the diversity and functioning of native ecosystems. Marine herbivores affect seaweed biomass and community structure in marine habitats across the globe. Consequently, herbivore-seaweed interactions are expected to be important for the establishment and invasion success of non-native seaweeds. To synthesize current knowledge of consumer effects on non-native seaweeds, we performed a meta-analysis on feeding preferences of native herbivores for non-native versus native seaweeds. Data were included from 35 studies, published from 1992–2015 and comprising 18 non-native seaweeds. Results showed that overall, native herbivores tended to prefer to feed on native rather than non-native seaweeds. Preferences were, however, variable across studies with significant differences between taxonomic and functional groups of seaweeds. In particular, filamentous red non-native seaweeds were of low palatability to native herbivores. No general feeding preferences were apparent between natives and non-natives for brown and green seaweeds, or for leathery and corticated seaweeds. In addition, we reviewed the existing studies on the effects of consumers on the performance of native and non-native seaweeds in invaded communities. This indicated that non-native seaweeds performed better than their native competitors in the presence of grazers, but in many cases had superior competitive abilities also in the absence of herbivory. To achieve a comprehensive evaluation of consumers' role in seaweed invasion success, future research should have a larger focus on manipulative community experiments, ideally on time scales that include seasonal changes and complete life cycles of the seaweeds.

Introduction

At any time, several thousand marine species are shuffled between biogeographical regions of the world's oceans (Johnson & Chapman 2007). Some of these species establish in their new communities and become widespread and abundant, being deemed invasive, with significant impacts on community composition and ecosystem properties (Williamson & Fitter 1996). The global number of non-indigenous seaweeds has reached more than 270 species (Williams & Smith 2007), many of them reported to negatively affect native seaweed communities in terms of cover, density and biodiversity (Schaffelke & Hewitt 2007, Engelen et al. 2015, Maggi et al. 2015). Identification of the

factors that control establishment and invasion success of non-native species is a key challenge in invasion ecology and important for risk assessment and management of non-indigenous seaweeds.

Herbivores have large influence on the abundance and community structure of both terrestrial and marine primary producers across ecosystems (e.g. Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Hawkins et al. 1992, Hay & Steinberg 1992, Burkepille & Hay 2008, Poore et al. 2012). Consequently, herbivore-plant interactions have long been suggested to be crucial also for the outcome of plant invasions. On the one hand, herbivores are recognized to contribute to biotic resistance against the establishment and proliferation of non-native plants (Elton 1958, Maron & Vila 2001). On the other hand, herbivore foraging has been suggested to drive invasions, when native herbivores preferably consume native over the non-native plant species. The latter argument forms the basis for the enemy release hypothesis (ERH), which states that non-native species become invasive since they escape the regulation of their co-evolved enemies in their native range and are less affected by enemies compared to the native competitors in their new range (Darwin 1859, Elton 1958, Keane & Crawley 2002). The reduced negative impact of herbivores is expected to give the non-native species a competitive advantage over the native plants in the community, leading to dominance and a biological invasion (Keane & Crawley 2002).

The concepts of biotic resistance and enemy release originate from terrestrial plant systems; the findings from these systems have been summarized in several reviews and meta-analyses (Colautti et al. 2004, Levine et al. 2004, Liu & Stiling 2006, Parker et al. 2006, Chun et al. 2010). Recently, Kimbro et al. (2013) published a meta-analysis on biotic resistance in marine environments, indicating negative effects of consumers on non-native marine primary producers. Seaweeds were only represented by seven studies in their analysis and seaweed data were analyzed together with data on a non-native salt marsh grass. Thus, a comprehensive quantitative synthesis of research on herbivore effects on non-native seaweeds is still lacking.

Seaweed communities are strongly dominated by generalist herbivores (Hawkins & Hartnoll 1983, Hawkins et al. 1992, Hay & Fenical 1992), which are more likely than specialists to include newly encountered species into their diet. Accordingly, generalist consumers have been suggested to counteract invasions by providing biotic resistance instead of facilitating invasions through enemy release (Parker & Hay 2005, Parker et al. 2006). There are, however, mechanisms by which non-native plants can escape generalist herbivores in their new range, especially by means of chemical defences (Wikström et al. 2006, Verhoeven et al. 2009, Forslund et al. 2010, Schaffner et al. 2011, Enge et al. 2012, Nylund et al. 2012). Seaweeds are known to be rich in secondary metabolites (Hay & Fenical 1992) and there is an increasing number of examples where potent chemical defences against native herbivores have been demonstrated in non-native seaweeds (Lemee et al. 1996, Lyons et al. 2007, Nylund et al. 2011, Enge et al. 2012). It is not known, however, if low palatability to generalist herbivores is a common trait of non-native seaweeds or if this trait is important for invasion success in seaweed communities.

The aim of this study was to review and synthesize current findings of consumer effects on non-native seaweeds. As part of the predictions of the ERH, we specifically explored via a meta-analysis whether non-native seaweeds are less palatable than native species, and thus generally experience a reduced impact by herbivores compared to native competitors. We further examined if there are differences among 1) seaweed taxonomic groups, 2) seaweed functional groups, 3) herbivore groups or 4) regions. Furthermore, we reviewed and summarized the literature that assessed the effects of herbivory on the competitive outcome between non-native and native seaweeds in a community.

Material and methods

Literature search and data extraction

Relevant studies for the meta-analysis were identified in the online database ISI Web of Science in August 2015, with no restrictions on publication year, using the following combination of search terms: ((introduced OR invasive OR non-native OR exotic OR alien OR non-indigenous) AND

(seaweed* OR alga* OR macroalga*) AND (herbivor* OR consum* OR *graz* OR enem* OR prefer*). In order to retrieve studies that tested non-native seaweeds but without specifying the species as non-native in the title or abstract, we performed an additional search for all non-native seaweeds listed in Williamson & Smith (2007) using the search terms: (('algal species name') AND (enem* OR herbivor* OR consum* OR graz*)). To determine if the seaweeds in these studies were non-native, we compared the study region with the reported natural distribution of the species. We further included three as yet non-peer-reviewed datasets (S.A. Wikström unpublished, K. Hill unpublished, S. Jakobsson unpublished). All titles and abstracts of the search results were screened for studies assessing feeding preferences or herbivore damage on non-native compared to native seaweeds, as well as for studies examining seaweed performances and competitive relationships between the non-native and native seaweeds in the presence and absence of herbivory. To be included in the final dataset, the studies had to meet the following criteria: 1) the investigated seaweed was non-native to the study region while the seaweeds used for comparison and the herbivores were native to the study region; 2) the study assessed herbivore preference, damage or their effects on both non-native and native seaweed performance under laboratory or field conditions in two- or multiple-species experiments using living algal material; 3) the experimental design included proper controls and presented all necessary measures for calculating the effect size. We excluded data of epifaunal abundances on non-native compared to native seaweeds because abundance may reflect habitat choice rather than food preference (e.g. work on refuges from predation: Duffy & Hay 1991, Enge et al. 2013). We also excluded data from no-choice feeding experiments since consumption in a no-choice situation can be confounded by compensatory feeding (Cruz-Rivera & Hay 2000). Furthermore, studies using gut content analysis of herbivores collected in the field were excluded because it was not possible to relate gut content to the availability of seaweeds in the field. Finally, studies where herbivores were preconditioned on one of the experimental seaweeds by either being specifically collected from or fed with only that seaweed prior to the experiments were also excluded.

For the retained studies the following data were compiled (see Table 1): seaweed species name, taxonomic and functional group, the study region and its corresponding climate region, the origin of the non-native seaweeds, herbivore species identity and phylum, as well as the experiment type (i.e. two- or multiple-choice). Mean values and measures of dispersion were extracted from figures using the WebPlotDigitizer software (Rohatgi 2015) or directly from text, tables or original datasets. All retrieved studies on herbivore feeding preference reported consumption or relative growth of the seaweeds as the response variable, which were either presented already corrected for autogenic changes of the seaweeds or together with the means of controls for autogenic changes. In the latter case, the consumption or relative growth data were corrected for the autogenic changes before values were entered into the database. To obtain a reference value for the native seaweeds in multiple-choice experiments, we calculated the average consumption of all native seaweeds and used their pooled variance as a measure of variability, which assumes the means of the populations to differ but their variances to be the same.

Meta-analysis

Hedges' d standardized mean difference (Hedges & Olkin 1985) was used as the effect size measure and was calculated as the difference between non-native and native seaweeds: $d = [(\bar{X}_{NN} - \bar{X}_N)/s]$, where \bar{X}_{NN} corresponds to the mean consumption of the non-native seaweed and \bar{X}_N to the mean consumption of the native species, s designates their pooled standard deviations and J is the small-sample-size bias correction factor. Positive Hedges' d values thereby reflect herbivore preference for the non-native seaweeds, while negative values reflect herbivore preference for the native seaweeds.

Many publications reported data of several independently performed two- or multiple-choice experiments using different native seaweed species and/or different herbivores, which resulted in up to 16 data entries from one study and for one non-native seaweed. To balance the influence of studies in the analyses and to decrease possible non-independence of these multiple entries, we

Table 1 Summary of the data on herbivore preference used in the meta-analysis

| Species | Functional group | Studies (number of data entries per study) | Studied regions | Climate region | Origin | Herbivore phylum | Herbivore species | Experiment type |
|--|------------------|---|--------------------------------------|------------------------|--------------|-------------------------------------|--|-----------------------------|
| Chlorophyta | | | | | | | | |
| <i>Caulerpa filiformis</i> | Corticated | Davis et al. 2005 (1); Cummings & Williamson 2008 (1) | SW Pacific | Subtropical | Indo-Pacific | Mollusca | <i>Turbo undulatus</i> ⁴ ; natural herbivore assemblage | Multiple-choice |
| <i>Caulerpa racemosa</i> var <i>cylindracea</i> ¹ | Corticated | Tomas et al. 2011a (1); Tomas et al. 2011b (1) | Mediterranean Sea | Subtropical | SW Pacific | Chordata; Echinodermata; | <i>Paracentrotus lividus</i> ; <i>Sarpa salpa</i> | Two-choice |
| <i>Codium fragile</i> ssp. <i>atlanticum</i> | Corticated | Trowbridge & Todd 1999 (1) | NE Atlantic | Temperate | NW Pacific | Mollusca | <i>Littorina littorea</i> | Two-choice |
| <i>Codium fragile</i> ssp. <i>tomentosoides</i> ² | Corticated | Prince & Leblanc 1992 (1); Trowbridge 1995 (3); Cruz-Rivera & Hay 2001 (1); Scheibling & Anthony 2001 (1); Chavanich & Harris 2002 (1); Levin et al. 2002 (2); Sumi & Scheibling 2005 (1); Hill (unpublished data) (2); Lyons & Scheibling 2007 (1); Jakobsson (unpublished data) (1) | NW Atlantic; NE Atlantic; SW Pacific | Temperate; Subtropical | NW Pacific | Arthropoda; Echinodermata; Mollusca | <i>Ampithoe longimana</i> ; <i>Cookia sulcata</i> ; <i>Evechinus chlonoticus</i> ; <i>Idotea granulosa</i> ; <i>Lacuna vincia</i> ; <i>Strongylocentrotus droebachiensis</i> ; <i>Turbo smaragdus</i> ⁵ | Two-choice; Multiple-choice |

Continued

Table 1 (Continued) Summary of the data on herbivore preference used in the meta-analysis

| Species | Functional group | Studies (number of data entries per study) | Studied regions | Climate region | Origin | Herbivore phylum | Herbivore species | Experiment type |
|--------------------------|------------------|--|-------------------------|------------------------|-------------|-------------------------------------|--|-----------------------------|
| Phaeophyceae | | | | | | | | |
| <i>Fucus evanesceus</i> | Leathery | Schaffelke et al. 1995 (1); Wikström et al. 2006 (2) | NE Atlantic | Temperate | N Circumpol | Arthropoda; Mollusca | <i>Idotea granulosa</i> ; <i>Littorina obtusata</i> | Two-choice; Multiple-choice |
| <i>Fucus serratus</i> | Leathery | Wikström et al. 2006 (1); Steinarsdóttir et al. 2009 (3); Wikström unpublished data (2) | NE Atlantic | Subpolar | N Circumpol | Arthropoda; Mollusca | <i>Gammarus obtusatus</i> ⁶ ; <i>Idotea granulosa</i> ; <i>Littorina littorea</i> ; <i>Littorina obtusata</i> | Two-choice |
| <i>Sargassum muticum</i> | Leathery | Britton-Simmons 2004 (1); Pedersen et al. 2005 (1); Hill (unpublished data) (2); Monteiro et al. 2009 (6); Strong et al. 2009 (1); Cacabelos et al. 2010 (4); Britton-Simmons et al. 2011 (1); Engelen et al. 2011 (3) | NE Atlantic; NE Pacific | Temperate; Subtropical | NW Pacific | Arthropoda; Echinodermata; Mollusca | <i>Aplysia punctata</i> ; <i>Dexamine spinosa</i> ; <i>Gammarus insensibilis</i> ; <i>Gibbula</i> spp.; <i>Hydrobia ulvae</i> ¹ ; <i>Idotea granulosa</i> ; <i>Lacuna vincta</i> ; <i>Littorina littorea</i> ; <i>Littorina obtusata</i> ; <i>Paracentrotus lividus</i> ; <i>Psammechinus militaris</i> ; <i>Stenosoma nadejda</i> ; <i>Strongylocentrotus droebachiensis</i> | Two-choice; Multiple-choice |

Continued

Table 1 (Continued) Summary of the data on herbivore preference used in the meta-analysis

| Species | Functional group | Studies (number of data entries per study) | Studied regions | Climate region | Origin | Herbivore phylum | Herbivore species | Experiment type |
|-----------------------------------|------------------|--|-------------------------|----------------|--------------|-------------------------|--|-----------------|
| <i>Undaria pinnatifida</i> | Leathery | Thornber et al. 2004 (1) | NE Pacific | Subtropical | NW Pacific | Arthropoda | <i>Pugettia producta</i> | Two-choice |
| Rhodophyta | | | | | | | | |
| <i>Acrothamnion preissii</i> | Filamentous | Tomas et al. 2011a (1) | Mediterranean Sea | Subtropical | Indo-Pacific | Echinodermata | <i>Paracentrotus lividus</i> | Two-choice |
| <i>Bonnemaisonia hamifera</i> | Filamentous | Hill (unpublished data (2)); Enge et al. 2012 (4) | NE Atlantic | Temperate | NW Pacific | Arthropoda; Mollusca | <i>Aplysia punctata</i> ; <i>Gammarus angulosus</i> ; <i>Gammarus locusta</i> ; <i>Idotea neglecta</i> ; <i>Littorina littorea</i> | Two-choice |
| <i>Gracilaria salicornia</i> | Corticated | Smith et al. 2004 (4) | N Pacific | Tropical | Indo-Pacific | Chordata | <i>Acanthurus blochii</i> ; <i>Acanthurus triostegus</i> ; juvenile scarids; <i>Zebrusoma flavescens</i> | Two-choice |
| <i>Gracilaria vermiculophylla</i> | Corticated | Weinberger et al. 2008 (2); Nejrup et al. 2012 (3) | Baltic Sea; NE Atlantic | Temperate | NW Pacific | Arthropoda; Mollusca | <i>Gammarus locusta</i> ; <i>Idotea balthica</i> ; <i>Littorina littorea</i> ; <i>Littorina</i> sp. | Two-choice |

Continued

Table 1 (Continued) Summary of the data on herbivore preference used in the meta-analysis

| Species | Functional group | Studies (number of data entries per study) | Studied regions | Climate region | Origin | Herbivore phylum | Herbivore species | Experiment type |
|---|------------------|---|--------------------------|----------------|---------------------------|----------------------|---|-----------------------------|
| <i>Heterosiphonia japonica</i> ³ | Filamentous | Low et al. 2015 (2); Sagerman et al. 2015 (2) | NE Atlantic; NW Atlantic | Temperate | NW Pacific | Arthropoda; Mollusca | <i>Gammarillus angulosus</i> ; <i>Gammarus locusta</i> ; <i>Idotea balhica</i> ; <i>Idotea granulosa</i> ; <i>Lacuna vincta</i> | Two-choice; Multiple-choice |
| <i>Lophocladia lallemandii</i> | Filamentous | Tomas et al. 2011a (1) | Mediterranean Sea | Subtropical | Indo-Pacific | Echinodermata | <i>Paracentrotus lividus</i> | Two-choice |
| <i>Mastocarpus stellatus</i> | Corticated | Yun & Molis 2012 (2) | NE Atlantic | Temperate | NE Atlantic | Arthropoda; Mollusca | <i>Idotea balhica</i> ; <i>Littorina littorea</i> | Two-choice |
| <i>Womersleyella setacea</i> | Filamentous | Tomas et al. 2011a (1) | Mediterranean Sea | Subtropical | Circum-equatorial | Echinodermata | <i>Paracentrotus lividus</i> | Two-choice |
| <i>Gracilaria salicornia</i> + <i>Acanthophora spicifera</i> + <i>Kappaphycus</i> sp. | Mixed | Stimson et al. 2007 (1) | N Pacific | Tropical | Indo-Pacific; NW Atlantic | Echinodermata | <i>Tripneustes gratilla</i> | Multiple-choice |

Note: The functional group division follows Littler & Littler (1984): filamentous = delicately branched, uniseriate to slightly corticated; corticated = coarsely branched, corticated; leathery = thick branched, heavily corticated or thick walled.

¹ *Caulerpa racemosa* var. *cylindracea* currently known as *Caulerpa cylindracea*; ² *Codium fragile* ssp. *tomentosoides* currently known as *Codium fragile* ssp. *fragile*; ³ *Heterosiphonia japonica* currently known as *Dasyssiphonia japonica*; ⁴ *Turbo undulatus* currently known as *Lunella undulata*; ⁵ *Turbo smaragdus* currently known as *Lunella smaragda*; ⁶ *Gammarus obtusatus* currently known as *Echinogammarus obtusatus*; ⁷ *Hydrobia ulvae* currently known as *Peringia ulvae*.

calculated a study-specific mean effect size for each herbivore species and non-native species across all experiments testing different combinations with native seaweeds in a study. In this way, we kept the resolution between the non-native seaweed and herbivore species, but reduced the problem of overweighing and consequent false precision estimates (Rothstein et al. 2013). We also calculated a study-specific mean effect size when experiments were repeatedly performed at different times during the year. In both cases, the study-specific mean effects were estimated using a fixed-effects model, which assumes the results of the different experiments in one study to vary only because of random sampling error. This procedure reduced the number of entries in the dataset with a factor of up to five for some publications and in total from 145 to 74 entries.

The meta-analysis on consumer preference for non-native versus native seaweeds was conducted using the metafor-package in R (Viechtbauer 2010) and the OpenMee software (Dietz et al. 2016). The weighted overall mean effect of herbivore preference for non-native or native seaweeds was calculated by a random-effects model using the restricted maximum-likelihood estimator for residual heterogeneity. Bootstrapped 95% confidence intervals were calculated for the overall mean effect size generated from 4999 iterations. To check the robustness of the meta-analysis outcome, we calculated the fail-safe number with the weighted method of Rosenberg (2005), which represents the number of additional studies with no effect needed to change the result of the meta-analysis from significant to non-significant. Publication bias was further examined with a funnel-plot and the rank correlation test for funnel plot asymmetry (Begg & Mazumdar 1994). The influence of outliers on the overall mean effects size was tested by evaluating the change of the overall effect when one study at a time was left out of the analysis. Since hypothesis-driven research tends to favour large effect sizes in support of the hypothesis in earlier publications, we examined temporal trends in the data with a cumulative meta-analysis sorted by publication year (Jennions & Møller 2002).

We used meta-regression with mixed-effects models and with a restricted maximum-likelihood estimator for residual heterogeneity to assess if the predefined covariables explained any of the observed heterogeneity and to explore their influence on consumer preference as well as differences between subgroups. Specifically, we tested how much of the observed heterogeneity the non-native seaweed itself accounted for, if there were differences in consumer preferences among phyla or functional groups of the non-native species, and if the climate region of the study site, herbivore phylum and experiment type influenced the study outcome. Origin and study region as covariables were omitted from these analyses since subgroups were often only represented by one or two species and few data entries in some of the subgroups, which were considered insufficient for a valid interpretation.

Only five studies that tested for consumer effects on the performance of non-native and native seaweeds on a community scale were identified, too few to perform a formal meta-analysis. However, findings of the few existing studies were summarized and discussed.

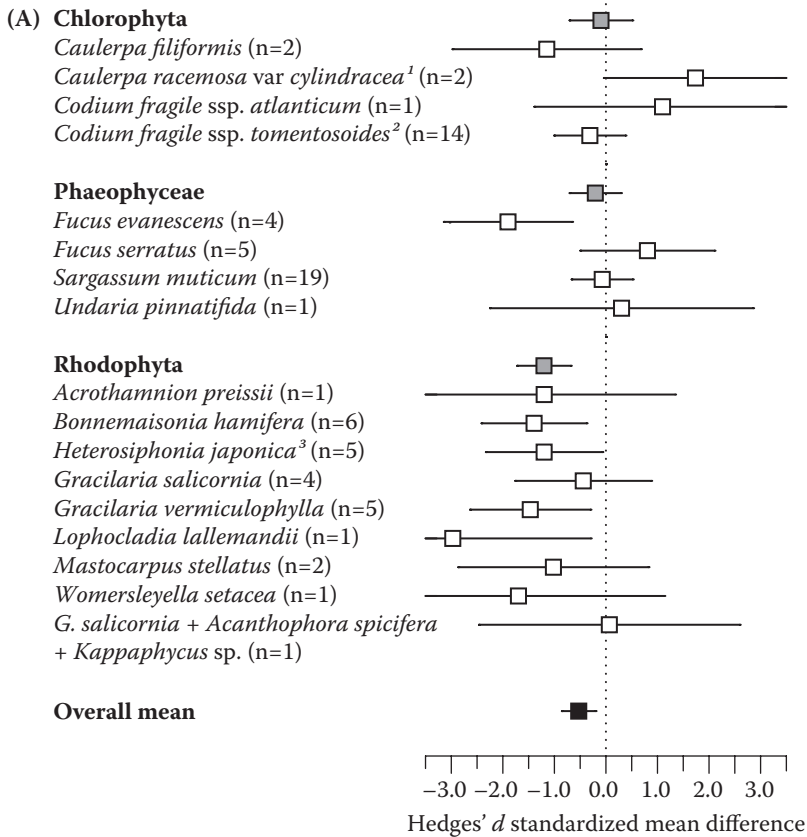
Results

The literature search identified 35 studies published from 1992–2015 that examined feeding preferences of native herbivores for non-native compared to native seaweeds. These studies addressed in total 18 non-native seaweed taxa: four green algae (Chlorophyta), four brown algae (Phaeophyceae) and ten red algae (Rhodophyta) (Table 1). This is comparable with the taxonomic composition of all registered non-native seaweeds reported by Williams & Smith (2007): of 276 taxa, 45 were green algae, 66 brown algae and 165 red algae. Accordingly, between 6–9% of all non-native seaweeds in each of the taxonomic groups were covered by our meta-analysis. All comparisons were made between non-native seaweeds and native seaweeds with the exception of one study with five data entries where the palatability of non-native seaweeds was compared to a seagrass species. By far the most intensively studied seaweeds in the context of feeding preference of herbivores were *Codium fragile* ssp. *tomentosoides* (currently accepted name *Codium fragile* ssp. *fragile*) and *Sargassum muticum*, which also resulted in the highest number of entries for these species in the meta-analysis

(Table 1). More than two thirds of the non-native seaweeds included in the meta-analysis have their original distribution in the north-west Pacific and Indo-Pacific, whereas the most intensively studied region of introduction was the north-east Atlantic (Table 1). Isopods and amphipods (Arthropoda), gastropods (Mollusca), sea urchins (Echinodermata) and herbivorous fish (Chordata) constituted the majority of the tested herbivores in the studies (Table 1).

Meta-analysis of consumer preference

The weighted overall mean effect was estimated to be -0.528 with a bootstrapped 95% CI = $(-0.872, -0.187)$. This effect was significantly different from zero ($p = 0.002$, Figure 1) and showed



| (B) Co-variable | Q _M | Q _E | I ² | R ² |
|-----------------|----------------|----------------|----------------|----------------|
| Species | 31.27* | 466*** | 92.33 | 17.53 |
| Phylum | 9.34** | 725*** | 92.95 | 11.72 |

Figure 1 (A) Forest plot of the estimated effect sizes (Hedges' d standardized mean difference) grouped by each non-native species (open squares) and by the phylum of the non-native species (grey squares). The black square indicates the overall mean effect size of feeding preferences. Error bars represent 95% confidence intervals. The numbers in brackets describe the number of dataset entries for each species. (B) The results of the meta-regression with the non-native seaweed or phylum of the non-native species as an explanatory variable in a random-effects model; * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$. ¹Currently accepted name *Caulerpa cylindracea*; ²Currently accepted name *Codium fragile* ssp. *fragile*; ³Currently accepted name *Dasyisiphonia japonica*.

that non-native seaweeds were on average less preferred by native herbivores compared to native seaweeds. The results of the different studies were, however, highly heterogeneous (residual heterogeneity among studies: $Q_{1,74} = 909.67$, $p < 0.001$, $I^2 = 93.8\%$). Including the predefined covariables in the model showed that the identity of the non-native seaweed, taxonomic and functional groups as well as the experiment type explained significant amounts of the observed heterogeneity (Figures 1 and 2). Residual heterogeneity was always high indicating that there may be other moderators not embraced by our analysis that influenced the outcome.

Grouping the non-native species by their taxonomic group revealed that only non-native red seaweeds were of low palatability to native herbivores, while the non-native green and brown seaweeds did not differ significantly in palatability compared to native seaweeds (Figure 1). Grouping according to functional groups suggested that only non-native filamentous seaweeds were less preferred, whereas the palatability of corticated or leathery non-native seaweeds did not differ from native counterparts (Figure 2). Due to the dataset structure, functional and taxonomic group were highly confounded: all green algae were corticated, all brown algae were leathery macrophytes and all filamentous algae were red seaweeds (Table 1). However, when functional groups were separately

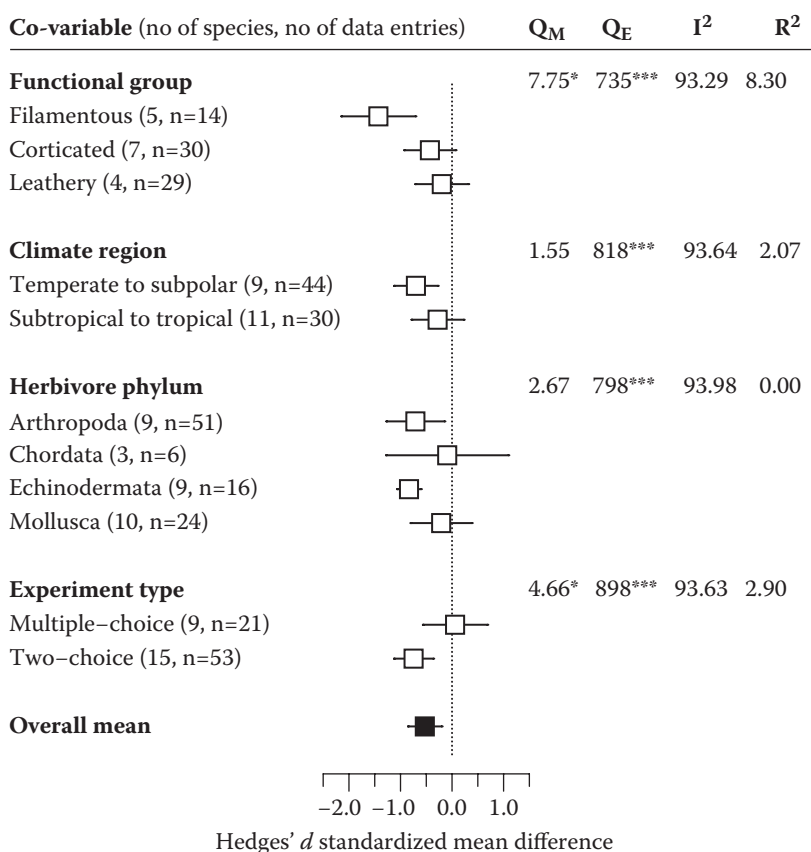


Figure 2 Forest plot of the estimated effect sizes (Hedges' d standardized mean difference) grouped by explanatory variables (open squares). The black square indicates the overall mean effect size of the dataset. Error bars represent 95% confidence intervals. The numbers in brackets describe the number of non-native species and the number of dataset entries represented by each subgroup. The statistics of the meta-regression of a random-effects model using functional group of the non-native seaweed, climate region and experiment type as an explanatory variable are displayed to the right; * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$.

tested for non-native red seaweeds, only filamentous seaweeds were again significantly less preferred ($Z_{\text{filamentous}} = -4.28$, $p < 0.001$; $Z_{\text{corticated}} = -1.80$, $p = 0.07$).

Analysis of the herbivore grouping revealed that arthropods and echinoderms found non-native seaweeds less palatable than native seaweeds, whereas molluscs and fish did not show any preference (Figure 2). Furthermore, herbivores from temperate to subpolar regions significantly preferred native seaweeds to non-native seaweeds, but herbivores from tropical or subtropical regions did not show a preference (Figure 2).

The experiment type had a significant influence on the effect size. In contrast to the two-choice experiments, the multiple-choice experiments, in which consumption of the non-native seaweed was compared to the averaged consumption of all native seaweeds, did not detect an overall significant feeding preference for native or non-native seaweeds (Figure 2).

Sensitivity analysis, publication bias and temporal trends

There was no indication that the results obtained from the meta-analysis lacked robustness. Exclusion of any data entry in the meta-analysis always resulted in similar overall mean effect size and confidence intervals (results not shown), which indicated that there were no serious outliers present. The cumulative meta-analysis by publication year showed that from the eighth data entry (2001), the overall mean effect size was constantly negative, oscillating between -0.628 and -0.302 , though the 95% confidence interval included zero over some periods (Figure 3). Furthermore, Rosenberg's fail-safe number was sufficiently large (4219) to conclude that the observed outcome was a reliable estimate of the overall effect size. Additionally, the funnel plot and rank correlation test for funnel plot asymmetry gave no indication that publication bias affected the observed outcome (rank correlation test, Kendall's $T = 0.098$, $p = 0.2196$, Figure 4).

Review of community studies

Our literature search identified nine studies that examined adult performance of non-native seaweeds in the presence and absence of consumers. Only five reported effects on cover or biomass for both the non-native species and native seaweeds. These studies included one green, two brown and two red algal taxa and are summarized in Table 2. All taxa were also covered by the meta-analysis of feeding preference.

In the presence of herbivores, the filamentous red alga *Bonnemaisonia hamifera* reached higher cover and its biomass increased in short-term community experiments under laboratory conditions. In the absence of herbivores, *B. hamifera* was an inferior competitor compared to the native red seaweeds in the community and decreased in abundance (Enge et al. 2013, Sagerman et al. 2014). In contrast, the filamentous red alga *Heterosiphonia japonica* (currently accepted name *Dasyisiphonia japonica*) dominated the community independent of herbivore presence due to its extreme growth rate (Sagerman et al. 2014). Compared to six native species, the leathery brown alga *Sargassum muticum* was the only seaweed that could maintain clear positive growth in the presence of herbivores in a short-term laboratory community experiment, but was also a superior competitor in the absence of herbivores (Engelen et al. 2011). Grazing had no effect on the cover of the corticated green alga *Codium fragile* ssp. *tomentosoides* (currently accepted name *Codium fragile* ssp. *fragile*) in a 13-week field experiment, while the native competitor *Laminaria longicruris* (currently accepted name *Saccharina longicruris*) could not persist and cover of turf algae strongly decreased under natural sea urchin densities. But again, *Codium fragile* ssp. *tomentosoides* had superior competitive abilities compared to *Laminaria longicruris* even in the absence of herbivores (Sumi & Scheibling 2005). On sea urchin barrens, grazing could not prevent canopy development of the leathery brown *Undaria pinnatifida* over a 30-month period, while the native canopy species did not exceed more than 0.7% cover (Valentine & Johnson 2005). In addition, the native canopy species showed inferior

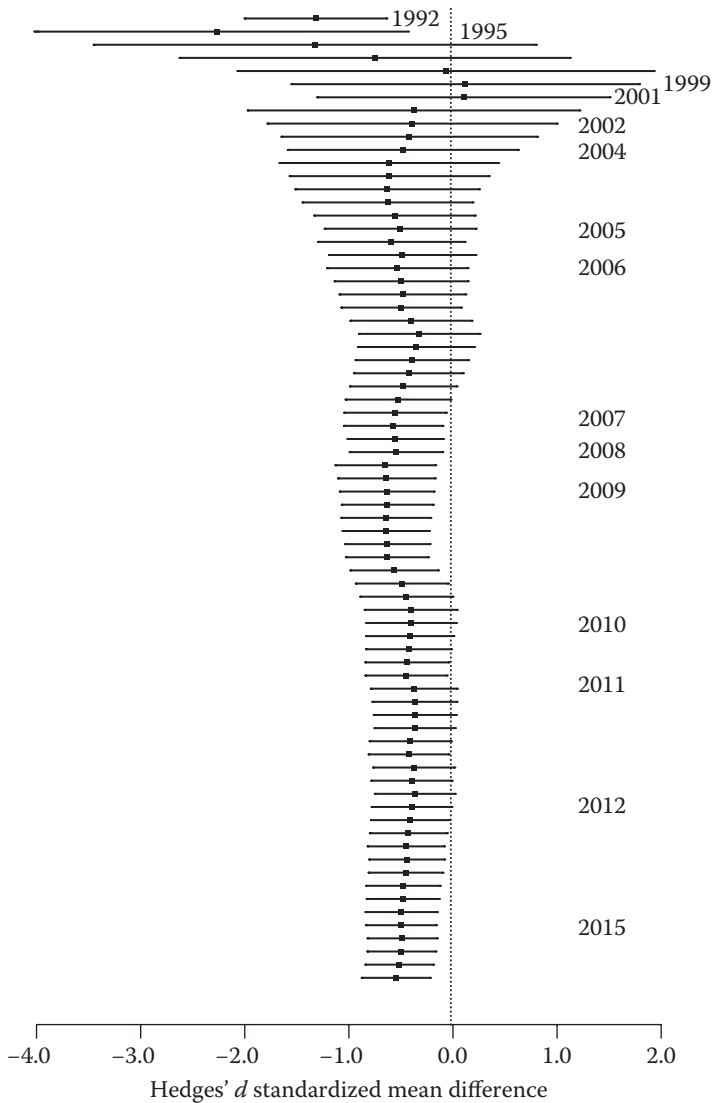


Figure 3 Forest plot of the cumulative meta-analysis of herbivore feeding preference between native and non-native seaweeds, ordered by publication year. Each data point represents the change of the estimated overall mean effect size (Hedges' *d* standardized mean difference) by adding the next newest entry into the meta-analysis. The dotted line indicates the absence of a significant effect. Error bars represent 95% confidence intervals.

competitive abilities compared to *U. pinnatifida* in the absence of herbivores (Valentine & Johnson 2005).

Discussion

Our meta-analysis showed that overall, non-native seaweeds tend to be less palatable than native seaweeds to herbivores in the new community. However, the meta-analysis also revealed considerable variability among the results of different studies. This variability could largely be explained by the identity of the seaweed taxon, indicating that the relative palatability of native compared

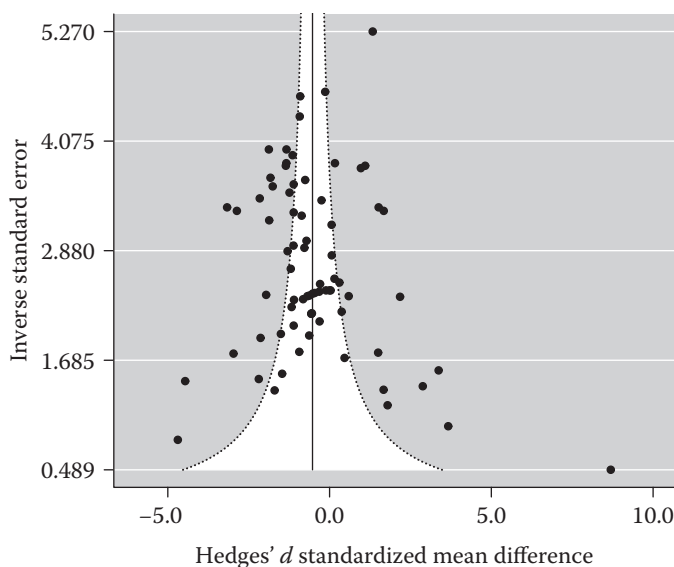


Figure 4 Funnel plot for the meta-analysis of feeding preferences using a random-effects model. Each data entry is represented by a circle showing the relation of the effect size (Hedges' d standardized mean difference) to its inversed standard error. The black line indicates the estimated overall mean effect and the white region represents the region in which 95% of the studies are expected to lie in the absence of biases and heterogeneity.

Table 2 Summary of community studies on herbivore effects on non-indigenous seaweeds

| Species | Taxonomic group | Functional group | Studies | Method |
|--|-----------------|------------------|--|-----------------------|
| <i>Codium fragile</i> ssp. <i>tomentosoides</i> ¹ | Chlorophyta | Corticated | Sumi & Scheibling 2005 | Field experiment |
| <i>Sargassum muticum</i> | Phaeophyceae | Leathery | Engelen et al. 2011 | Laboratory experiment |
| <i>Undaria pinnatifida</i> | Phaeophyceae | Leathery | Valentine & Johnson 2005 | Field experiment |
| <i>Bonnemaisonia hamifera</i> | Rhodophyta | Filamentous | Enge et al. 2013, Sagerman et al. 2014 | Laboratory experiment |
| <i>Heterosiphonia japonica</i> ² | Rhodophyta | Filamentous | Sagerman et al. 2014 | Laboratory experiment |

Note: The Functional group classification follows Littler & Littler (1984): filamentous = delicately branched, uniseriate to slightly corticated; corticated = coarsely branched, corticated; leathery = thick branched, heavily corticated or thick walled.

¹ currently accepted name *Codium fragile* ssp. *fragile*

² currently accepted name *Dasyisiphonia japonica*

to non-native seaweeds differs between the groups of red, brown and green seaweeds. It was only for reds, but not for the brown and green seaweeds, that the meta-analysis demonstrated an overall difference in herbivore preference between native and non-native species. Furthermore, the meta-analysis revealed that filamentous non-native species, which were all red seaweeds in our analysis, tended to be of low palatability to native herbivores.

Feeding preference of herbivores is positively correlated to the nutritional quality and the shelter provided by the seaweed, and seaweeds can in turn deter herbivores by structural and chemical defences (Lubchenco & Gaines 1981, Hay & Fenical 1992). The low herbivore preference for non-native filamentous algae is an unexpected result because filamentous algae are commonly regarded to be palatable and highly susceptible to most consumers (Littler & Littler 1980, Steneck & Watling

1982, Littler et al. 1983). Consequently, this group could be expected to face a higher degree of consumptive biotic resistance in new regions, compared to non-native seaweeds from other functional groups. Our result matches recent findings suggesting that leathery and foliose algae are more susceptible to herbivores than filamentous or corticated algae (Poore et al. 2012), which indicates that structural traits, such as tissue toughness, is far from always a determining factor for food choice of herbivores and that feeding preferences are driven by other seaweed traits.

The presence of chemical defences can explain low palatability of certain seaweeds to marine herbivores (Hay & Fenical 1992, Pavia et al. 2012). Accordingly, it has been postulated that chemical defences can protect non-native seaweeds, as well as vascular plants, from being attacked by native herbivores in a new region, either by comparatively high defence concentrations or by molecular structures that are evolutionarily novel to the native herbivores (Cappuccino & Arnason 2006, Wikström et al. 2006, Verhoeven et al. 2009, Enge et al. 2012). Red seaweeds in particular produce an immense diversity and high quantities of often halogenated secondary metabolites, which have been frequently demonstrated to possess effective antimicrobial (Persson et al. 2011, Nylund et al. 2013), antifouling (Dworjanyn et al. 2006), allelopathic (Svensson et al. 2013) and antiherbivore activities (Kladi et al. 2005, Cabrita et al. 2010, Enge et al. 2012). The diversity of chemical defence compounds in red algae may explain why non-native red seaweeds showed especially low palatability in our meta-analysis.

The establishment of a specific chemical basis for a low preference of potential native consumers for an introduced organism is, however, a demanding task and marine examples are still rare. Evidence for chemical defences against native herbivores has so far only been provided for a few non-native seaweed species. The green algae, *Caulerpa taxifolia* and *C. racemosa*, produce caulerpenyne with effects on sea urchins (Amade & Lemée 1998, Dumay et al. 2002). *Codium fragile* ssp. *fragile* (= *Codium fragile* ssp. *tomentosoides*) possesses wound-activated defences involving dimethylsulfoniopropionate (DMSP), which deters native sea urchins (Lyons et al. 2007). The arctic brown alga, *Fucus evanescens**, contains significantly higher concentrations of phlorotannins (polyphenolic defence compounds) than native fucoids in its new range, deterring native isopods and molluscs (Wikström et al. 2006, Forslund et al. 2010). The highly invasive red alga, *Gracilaria vermiculophylla*, produces prostaglandins, hydroxylated fatty acids and arachidonic acid-derived lactones on wounding, which provides resistance against native isopods and molluscs (Nylund et al. 2011, Hammann et al. 2016). Another red seaweed, the filamentous *Bonnemaisonia hamifera*, produces volatile brominated compounds that provide defence against native isopods, gammarids and ophistobranch consumers (Enge et al. 2012). These examples show that chemical defence can explain the low palatability of some non-native seaweeds, but further studies are needed before it can be concluded that chemical defence is a common trait of low-preferred non-native seaweeds (especially of the filamentous red algae).

Notably, two of the species for which chemical defences have been characterized (*Caulerpa racemosa* and *Codium fragile* ssp. *tomentosoides*) were not consistently of low preference to native herbivores in our meta-analysis. In both cases, the chemical defence compound was only documented to be active against one herbivore species, while multiple herbivores were tested in the feeding preference experiments. A specific chemical defence is usually not effective against all herbivore species, since herbivores can adapt to and/or circumvent the effects of secondary metabolites (Sotka, 2005). Furthermore, concentrations and the effectiveness of the chemical defence compounds can vary between seaweed and herbivore populations (Pavia et al. 2003, Sotka 2005), which makes it

* *Fucus evanescens* may have expanded its range naturally, but available evidence suggests that the spread of this species to southern Scandinavia and the British Isles was aided by human transport. It exhibits a disjunct distribution with new occurrences that were discovered in harbours in the beginning of the 20th century, making introduction from shipping plausible. Thus, we chose to include *Fucus evanescens* in the definition of a non-native species that we used in the literature search, i.e. a species that has been translocated to a new range by humans.

important that the palatability of non-native species introduced into several regions are tested with a set of the native herbivores that are relevant in the new regions.

Herbivore preference can be a first indicator for plant performance and competitive ability, but cannot be directly translated into community composition and population dynamics under natural conditions. We found that studies using long-term community experiments assessing the effects of consumers on non-native seaweeds in interaction with native seaweeds are essentially lacking. The few existing studies included in our review showed that performance of non-native seaweeds can be increased, equal or reduced in the presence of herbivores. To date, the most rigorous example of a successful seaweed invasion based on chemical defence concerns the filamentous red alga *Bonnemaisonia hamifera* (Figure 5). The documented chemical defence (1,1,3,3-tetrabromo-2-heptanone) provides this relatively poor competitor (in the absence of native herbivores), with a strong competitive advantage in its new range in the presence of native herbivores (Enge et al. 2013, Sagerman et al. 2014). In addition, the same brominated compound inhibits the recruitment of native algal competitors (Svensson et al. 2013) and reduces bacterial load (Nylund et al. 2008). Thus, the multiple ecological benefits of this compound outweigh the cost of its production for the invader in the new range (Nylund et al. 2013). In some of the other studies the non-native seaweeds often performed better than their native competitors in the presence of herbivores, but the non-native species were superior competitors also in the absence of herbivores. Thus, the extent to which low herbivore preference contributes to invasion success of non-native seaweeds remains elusive. There is a need for more studies on the effects of herbivores on non-native seaweed populations, ideally experiments that include seasonal changes and complete life cycles of the seaweed and grazers. This is a challenging task in marine environments with species with complex life cycles.

In conclusion, the results of our meta-analysis show that low palatability does not seem to be a universal trait among non-native seaweeds and only certain seaweeds escape native herbivores in

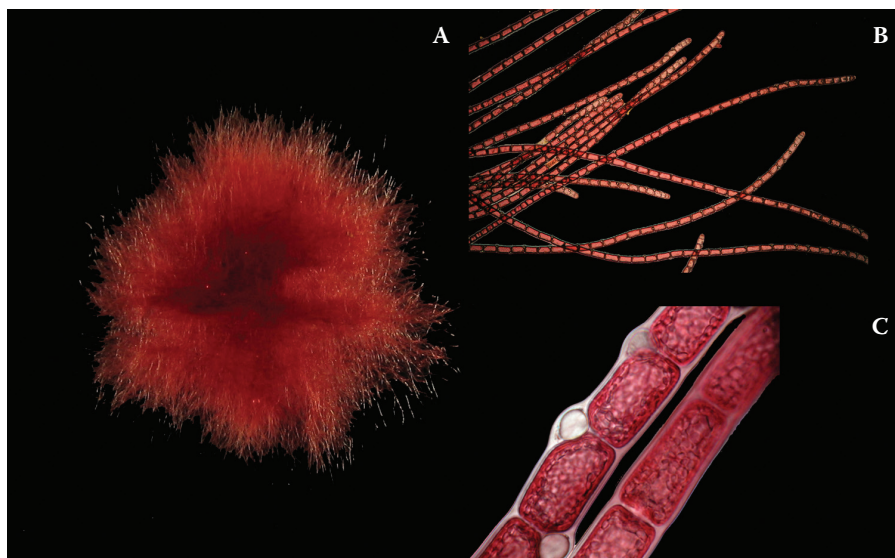


Figure 5 The invasive filamentous red seaweed *Bonnemaisonia hamifera*, which produces a potent chemical defence (1,1,3,3-tetrabromo-2-heptanone) that makes it unpalatable to native herbivores in the north Atlantic, thereby providing it with a strong competitive advantage over native seaweeds in its new range. (A) Tetrasporophytic phase, growing as small turfs, which consist of numerous sparsely branched filaments (B). Filaments are one cell-layer thick and have numerous gland cells, containing chemical defences, located between the vegetative cells (C). (From Nylund et al. 2008.)

their new range. Accordingly, the prediction of the enemy release hypothesis that introduced species are less attacked by herbivores than their native counterparts in the new range (Keane & Crawley 2002), does not hold for all non-native seaweeds. Interestingly, we found that non-native filamentous red seaweeds tend to be especially less palatable to herbivores. This is an important finding considering the majority of seaweed introductions are filamentous or corticated red algae (Williams & Smith 2007). Due to their morphology, these species can often be cryptic or less apparent compared to larger brown and green seaweeds. Probably, therefore, they are less frequently studied and often overlooked in their community impacts, even though effects on biodiversity and ecosystem processes have been proven (Schaffelke & Hewitt 2007, Sagerman et al. 2014). The low preference for many non-native filamentous red algae indicates that low impact of herbivores may contribute to invasion success in this group. However, to assess if consumers play a crucial role in seaweed invasions, future research should focus on examining consumer impacts on competitive interactions between non-native and native seaweeds.

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