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Chapter 6

Non-native Seaweeds Drive Changes in Marine Coastal Communities Around the World

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Abstract We conducted a bibliographic survey, adding 69 taxa to a published list of 277 seaweeds, thereby updating the total worldwide list of non-native and cryptogenic seaweeds to 346. *Polysiphonia* Greville and *Hypnea* J.V. Lamouroux species were the most common taxa on this list, and the Mediterranean Sea and the NE Atlantic bioregions have received most of the 346 taxa. The most important vectors that carry non-native seaweeds are hull fouling and the transport of aquaculture products including ‘blind passengers’. Once a seaweed has arrived in a new location, it can establish a permanent population and spread through natural dispersal or human activity. Non-native seaweeds have negative impacts on native species through competition, habitat destruction and keystone competition, but also positive impacts through habitat formation, food provision and cascading habitat formation. Quantitative meta-analyses have shown that invasive seaweeds typically have a negative effect on local plants, but neutral or positive effects on animal communities. New meta-analyses presented here indicate that impacts increase with the abundance of non-native seaweeds and that non-native seaweeds may increase sample similarity in invaded plant communities, but not in animal communities. The literature on the impact of non-native seaweeds is extensive, but most studies have focused on a few high-profile species. Comprehensive analyses should be

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done for more species to allow for better predictions. We conclude that non-native seaweeds have altered shallow coastal communities in most biogeographical regions, and impacts will likely increase along with increases in human populations, transport and associated stressors.

Keywords Invasion impact · Invasion success · Meta-analysis · New invasions · Density-dependent effects · Trophic matching hypothesis

6.1 Introduction—Scope of Seaweed Invasions

Non-native seaweeds are marine macroalgae that have arrived at new locations aided by human activity, either deliberately or accidentally. Today, non-native seaweeds comprise hundreds of species distributed in the photic zone throughout the world's major biogeographical regions. Many non-native seaweeds are 'foundation species' (Dayton 1972) and function as 'ecosystem engineers' (Jones et al. 1994), directly or indirectly affecting the availability of resources to other species by creating, modifying and maintaining habitats (Wallentinus and Nyberg 2007; Thomsen et al. 2010). Consequently, non-native seaweeds play key ecological and biogeochemical roles in their new marine ecosystems, sometimes controlling biodiversity, ecosystem functioning and energy flow (Williams and Smith 2007).

The success of a non-native seaweeds is typically considered a staged process that depends on uptake from a donor-region, transport, arrival and release to a receiver-region, local establishment and proliferation, population growth and regional spread and range expansion (Sakai et al. 2001; Bates et al. 2014). For each of these stages, a non-native seaweed has to overcome a series of physical, physiological, demographic and biological barriers and filters that act as a constant sink for new species and individuals. In this chapter, we first review which seaweed species have invaded various regions and then provide a brief overview of the two main approaches in invasion ecology, 'success' and 'impact' studies and their related frameworks and working hypotheses. We subsequently provide examples of impacts on local populations and evaluate existing quantitative syntheses of invasion impacts and identify current research gaps. We then address key research gaps using meta-analysis to test whether invasive seaweeds have density-dependent effects and decrease variability in community similarity. This 'case study section' is therefore more detailed than the rest of this review chapter. Finally, we provide a summary of the major findings from the chapter. Our focus is on non-native seaweeds, but we also comment on non-native seagrasses (marine or estuarine angiosperms) and terrestrial halophytes (salt marsh and mangrove angiosperms), since they interact with invasive seaweeds in intertidal or brackish habitats (e.g. Thomsen et al. 2012; Williams and Grosholz 2008).

We use the term ‘non-native’ (=alien, non-indigenous, exotic, introduced) to define species that live outside their native distributional range. We include species that have dispersed by their own means through man-made canals (e.g. Lessepsian migration where non-native species swim or drift through the Suez Canal) but not new species that arrived by their own dispersal across natural barriers, and only survive due to climate changes. We characterise non-native species that are ‘highly successful’ (e.g. spread rapidly and establish abundant populations) or have a ‘strong impact’ on resident populations or ecosystems as ‘invasive’, but acknowledge the ambiguities and lack of a clear definition for when or where non-native species are invasive or not (indeed, it is more appropriate to rank non-natives according to their ‘relative invasiveness’ within the success and impact criteria). We define cryptogenic species as species that are of uncertain origin: for these species, detailed taxonomic, biogeographical and molecular analyses are required to determine whether they are non-natives. Throughout this chapter, we describe non-native and invasive ‘species’, but we assert that data are always collected from specific populations (genotypes) that represent a limited subset of a species’ gene pool. Researchers should, of course, be cautious when success and impact of a non-native genotype is predicted from a study conducted on a different genotype.

6.2 Research on and Numbers of Non-native Seaweeds

Invasions by marine primary producers have been described by scientists for a long time. For example, the Danish oceanographer Carl Emil Hansen Ostenfeld described the invasion of the planktonic diatom *Biddulphia (Odontella) sinensis* Greville into the North Sea in 1903, probably transported by ships (Ostenfeld 1908). Over 50 years ago, Charles Elton, in his seminal book on biological invasions, described dramatic ecosystem changes associated with *Spartina* von Schreber invasions, converting marine intertidal mudflats to salt marshes on massive scales (Elton 1958). Elton even applied invasion patterns to support the notion that ‘Falkenbergia rufolanosa’ was the tetrasporophytic phase of *Asparagopsis armata* Harvey, because these two seaweed morphologies showed simultaneous spread into the north-east Atlantic and Mediterranean Sea in the 1920s–1950s (originating from south-western Australia). However, research on seaweed invasions did not take off until the 1990s. A ‘topic’ search in the Web of Science using classic invasion terminology [TS = ((invasion* or exotic* or non-native* or alien*) and (seaweed* or macro-alga* or macroalga*))] revealed that the first scientific paper on the topic was published in 1973 (Wassman and Ramus 1973) followed by 2 papers in the 1980s (Russell 1981; Dale 1982), 37 from 1990 to 1999, 210 from 2000 to 2009 and 235 papers from 2010 to 2015. This search does not include all relevant references—and includes a few less relevant studies—but nevertheless documents that few studies predated the 1990s. The growing number of primary research

studies on seaweed invasions has been reviewed in some detail (e.g. Thomsen et al. 2009b; Williams and Smith 2007; Schaffelke et al. 2006; Inderjit et al. 2006; Johnson and Chapman 2007). The most comprehensive of these reviews was by Williams and Smith (2007), describing 277 seaweed taxa introduced around the world including a few unidentified taxa within particular genera (e.g. *Bryopsis* J.V. Lamouroux., *Ulva* Linnaeus subspecies (e.g. *Codium fragile* ssp. *scandinavicum* P.C. Silva and *tomentosoides* (van Goor) P.C. Silva) and taxa of cryptogenic origin (including a few that probably are natives, e.g. *Alaria esculenta* (L.) Greville and *Saccharina ochotensis* (Miyabe) C.E. Lane, C. Mayes, Druehl and G.W. Saunders that are likely natives in Denmark).

Williams and Smith's (2007) tally is almost a decade old and we considered it timely to conduct a bibliographic survey to update their list. From this survey, we identified 69 taxa not included on the list (Table 6.1) expanding the number of non-native and cryptogenic seaweed taxa globally to 346. This list includes several cryptogenic taxa that future studies may reclassify as native, but we suggest that the 346 taxa still represent a conservative estimate because (1) our search may have missed studies, (2) seaweeds may have been introduced to new regions prior to modern science, (3) morphologically similar non-native and native species may co-occur and remain taxonomically cryptic, (4) under-studied regions can include non-native taxa that are (5) poorly described, (6) difficult to identify, (7) rare or (8) have invaded inaccessible areas and habitats. The 346 seaweeds are represented by 61 Chlorophyceae, 77 Phaeophyceae and 208 Rhodophyceae derived from a global species pool of ca. 2400 Chlorophyceae, 1800 Phaeophyceae and 6300 Rhodophyceae. The seaweed genera with most invasive taxa were *Polysiphonia* Greville (15 taxa), *Hypnea* J.V. Lamouroux (13), *Codium* Stackhouse and *Caulerpa* J.V. Lamouroux (11 each) and *Gracilaria* Greville (10) and the most invaded bioregions were the Mediterranean sea (160 taxa), followed by NE Atlantic (93), oceanic islands (73) Australasia (66), NW Atlantic (34) and the NE Pacific (33) (Fig. 6.1).

Finally, we note that in addition to the 346 seaweeds, at least four seagrasses (*Zostera japonica* J.V. Lamouroux, *Zostera tasmanica* Martens ex Ascherson, *Halophila stipulacea* (Forsskål) Ascherson, *H. Halophila decipiens* Ostenfeld), 6 mangroves (*Lumnitzera racemosa* Wild, *Sonneratia caseolaris* (Linnaeus), *Sonneratia apetala* Buch-Ham, *Bruguiera gymnorhiza* (L.) Lam., *Bruguiera sexangula* (Lour.) Poiret, *Rhizophora mangle* Linnaeus) and 10 salt marsh taxa (*Spartina alterniflora* Loiseleur-Deslongchamps., *S. anglica* C.E. Hubb, *S. patens* (Ait.) Muhl., *S. densiflora* Brögelmann., *S. alterniflora* × *foliosa* von Trinius., *S. densiflora* × *foliosa*, *Phragmites australis* (Cav.) von Trinius ex von Steudel., *Elymus athericus* (Link) Kerguelen, *Cotula coronopifolia* Linnaeus, *Ipomoea cairica* (L.) Sweet) have invaded coastlines around the world (Williams 2007; Fourqurean et al. 2010; Chen et al. 2009; Ren et al. 2009; Krauss and Allen 2003; Adam 1990).

Table 6.1 Bibliographic survey of non-native and cryptogenic seaweeds not included in Williams and Smith (2007)

| Taxa (Phyla) | Invaded bioregion | Reference |
|---|-------------------|---------------------------------------|
| <i>Aglaothamnion cordatum</i> (Børgesen) Feldmann-Mazoyer (R) | Islands | Micael et al. (2014) |
| <i>Anotrichium okamuræ</i> Baldock (R) | Med. | Zenetos et al. (2010) |
| <i>Antithamnion hubbsii</i> E.Y. Dawson (R) | Med. | Zenetos et al. (2010) |
| <i>Antithamnionella boergesenii</i> (Cormaci and G. Furnari) Athanasiadis (R) | Islands | Micael et al. (2014) |
| <i>Asparagopsis taxiformis</i> Delile Trevisan de Siant-Léon Lineage 3 (R) | Multiple, unknown | Dijoux et al. (2014) |
| <i>Asparagopsis taxiformis</i> Delile Trevisan de Siant-Léon Lineage 4 (R) | NEP | Dijoux et al. (2014) |
| <i>Botrytella cf. parva</i> (Takamatsu) H.S. Kim (O) | Med. | Zenetos et al. (2010) |
| <i>Caulerpa racemosa</i> var. [<i>lamourouxii</i>] <i>f.</i> <i>requinii</i> (Monagne) Weber-van Bosse (C) | Med. | Zenetos et al. (2010) |
| <i>Caulerpa racemosa turbinata</i> (J. Agardh) <i>Eubankuvifera</i> (J. Agardh) C. Agardh (C) | Med. | Zenetos et al. (2010) |
| <i>Caulerpa taxifolia distichophylla</i> (Sonder) Verlaque, Huisman and Procaccini (C) | Med. | Jongma et al. (2013) |
| <i>Caulerpa webbiana</i> Montagne (C) | Islands | Micael et al. (2014) |
| <i>Ceramium cingulatum</i> Weber-van Bosse (R) | Islands | Micael et al. (2014) |
| <i>Ceramium gaditanum</i> (Clemente) Cremades (R) | Islands | Micael et al. (2014) |
| <i>Chondracanthus</i> Kützing sp. (R) | NE Atlantic | Mineur et al. (2012) |
| <i>Chondria dasyphylla</i> (Woodward) C. Agardh (R) | Islands | Micael et al. (2014) |
| <i>Cladophora hutchisioides</i> C. Hoek and Wormersley (C) | Med. | Zenetos et al. (2010) |
| <i>Cladophora ruchingeri</i> (C. Agardh) Kützing (C) | Australasia | Pochon et al. (2015) |
| <i>Cladophoropsis membranacea</i> (Hofman Bang ex C. Agardh) Børgesen (C) | Islands | Micael et al. (2014) |
| <i>Cladostephus spongiosus</i> F. <i>hedwigioides</i> (Bory de Saint-Vincen) Prud'homme van Reine (O) | NE Pacific | Mazariegos-Villareal et al. (2010) |
| <i>Codium arabicum</i> Kützing (C) | Med. | Hoffman et al. (2011) |
| <i>Codium effusum</i> (Rafinesque) Delle Chiaje (C) | Islands | Micael et al. (2014) |
| <i>Codium parvulum</i> (Bory de Saint Vincent ex Audoin) P.C. Silva (C) | Med. | Zenetos et al. (2010) |
| <i>Ctenosiphonia hypnoides</i> (Welwitsch ex Agardh) Falkenberg (R) | Islands | Micael et al. (2014) |

(continued)

Table 6.1 (continued)

| Taxa (Phyla) | Invaded bioregion | Reference |
|--|--------------------------|-----------------------------|
| <i>Erythrodermis traili</i> (Holmes ex Batters) Guiry and Garbary (R) | Islands | Micael et al. (2014) |
| <i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh (R) | Islands | Micael et al. (2014) |
| <i>Fredericqia deveauniensis</i> Mags, Le Gall, Mineur, Provan and G.W. Saunders (R) | NW Atlantic, NE Atlantic | Maggs et al. (2013) |
| <i>Gracilariopsis chorda</i> (Holmes) Ohmi (R) | NE Atlantic | Mineur et al. (2012) |
| <i>Grateloupia asiatica</i> S. Kawaguchi and H. W. Wang (R) | Med. | Zenetos et al. (2010) |
| <i>Grateloupia minima</i> P.L. Crouan and H.M. Crouan (R) | Med. | Zenetos et al. (2010) |
| <i>Grateloupia subpectinata</i> Holmes (R) | Med. | Zenetos et al. (2010) |
| <i>Grateloupia yinggehaiensis</i> H.W. Wang and R.X. Luan (R) | Med. | Wolf et al. (2014) |
| <i>Halimeda</i> sp. J.V. Lamouroux (C) | Islands | Sissini et al. (2014) |
| <i>Halitilon virgatum</i> (Zanardini) Garbary and H.W. Johansen (R) | Islands | Micael et al. (2014) |
| <i>Hydropuntia perplexa</i> (K. Byrne and Zuccarello) Conkin (R) | Islands, Australasia | Conklin et al. (2014) |
| <i>Hypnea anastomosans</i> Papenfuss, Lipkin and P.C. Silva (R) | NE Atlantic | Tsiamis and Verlaque (2011) |
| <i>Hypnea flagelliformis</i> Greville ex J. Agardh (R) | Islands, Med. | Micael et al. (2014) |
| <i>Hypnea flexicaulis</i> Y. Yamagishi and M. Masuda (R) | Med. | Wolf et al. (2011) |
| <i>Hypnea stellulifera</i> (C. Agardh) Kützing (R) | SW Atlantic | de Jesus et al. (2014) |
| <i>Jania longifurca</i> Zanardini (R) | Islands | (Micael et al. 2014) |
| <i>Laurencia chondrioides</i> Børgesen (R) | Med. | Hoffman et al. (2014) |
| <i>Laurencia dendroidea</i> J. Agardh (R) | Islands, Med. | Micael et al. (2014) |
| <i>Leathesia marina</i> (Lyngbe) Decaisne (O) | Islands | Micael et al. (2014) |
| <i>Lomentaria flaccida</i> Tanaka (R) | Med. | Zenetos et al. (2010) |
| <i>Lophosiphonia reptabunda</i> (Suhr) Kylin (R) | Islands | Micael et al. (2014) |
| <i>Microspongium tenuissimum</i> (Hauck) A.F. Peters (O) | Med. | Zenetos et al. (2010) |
| <i>Nemalion vermiculare</i> Suringar (R) | Med. | Zenetos et al. (2010) |
| <i>Neomeris annulata</i> Dickie (C) | Med. | Zenetos et al. (2010) |
| <i>Nitophyllum stellatocorticatum</i> Okamura (R) | Med. | Zenetos et al. (2010) |
| <i>Padina antillarum</i> Kützing Piccone (O) | Med. | Zenetos et al. (2010) |
| <i>Palisada maris-rubri</i> (K.W. Nam and Saito) K.W. Nam (R) | Med. | Zenetos et al. (2012) |

(continued)

Table 6.1 (continued)

| Taxa (Phyla) | Invaded bioregion | Reference |
|--|--|-----------------------------|
| <i>Papenfussiella kuromo</i> (Yendo) Inagaki (O) | Islands | Micael et al. (2014) |
| <i>Petalonia binghamiae</i> (J. Agardh) K.L. Vinogradova (O) | Islands | Micael et al. (2014) |
| <i>Polyopes lancifolius</i> (Harvey) Kawaguchi and Wang (R) | NE Atlantic | (Mineur et al. 2009) |
| <i>Polysiphonia 'tepida'</i> Holenberg (R) | Islands | Carlton and Eldredge (2015) |
| <i>Polysiphonia schneideri</i> B. Stuercke and D.W. Freshwater (R) | NE Atlantic | Diaz-Tapia et al. (2013) |
| <i>Ptilothamnion pluma</i> (Dillwyn) Thuret (R) | Islands | Micael et al. (2014) |
| <i>Pylaiella littoralis</i> (L.) Kjellman (O) | Med. | Zenetos et al. (2010) |
| <i>Pyropia suborbiculata</i> (Kjellman) J.E. Sutherland, H.G. Choi, M.S. Hwang and W.A. Nelson (R) | Med., Australasia, Island, NE, SW, NW Atlantic | Verges et al. (2013) |
| <i>Rugulopteryx okamurae</i> ((E.Y. Dawson) I. K. Hwang, W.J. Lee and H.S. Kim O) | Med. | Verlaque et al. (2009) |
| <i>Sphacelaria fusca</i> (Hudson) S.F. Gray (O) | Islands | Micael et al. (2014) |
| <i>Sphacelaria tribuloides</i> Tribuloides (O) | Islands | Micael et al. (2014) |
| <i>Sphaerotrichia firma</i> (Gepp) A.D. Zinova (O) | Med. | Zenetos et al. (2010) |
| <i>Spongoclonium caribaeum</i> Børgesen) M. J. Wynne (R) | Islands, Med. | Micael et al. (2014) |
| <i>Spyridia 'filamentosa'</i> Clade A (Wulfen) Harvey (R) | Islands | Carlton and Eldredge (2015) |
| <i>Spyridia 'filamentosa'</i> Clade B (R) | Islands | Carlton and Eldredge (2015) |
| <i>Udotea argentea</i> Zanardini (C) | Islands | Carlton and Eldredge (2015) |
| <i>Ulva obscura</i> Kützing (C) | Med. | (Zenetos et al. 2010) |
| <i>Ulva ohnoi</i> M. Hiraoka and S. Shimada (C) | Islands | Carlton and Eldredge (2015) |
| <i>Uronema marinum</i> Wormersley (C) | Med. | Zenetos et al. (2012) |

Phyla are shown in brackets, i.e. Rhodophyta (R), Ocrophyta (O) and Chlorophyta (C). Med. = Mediterranean Sea. Islands = a variety of isolated oceanic islands, e.g. the Azores. We followed Dijoux (2014) on the *Asparagopsis* Montagne complex, assuming that Williams and Smith (2007) included Lineage 2 in their review

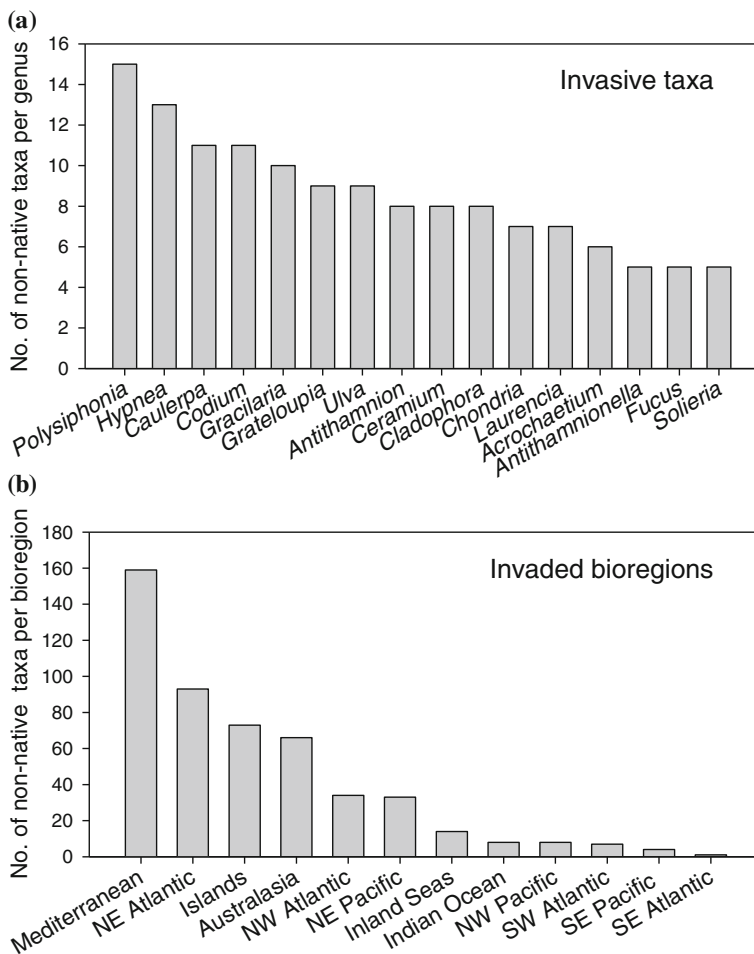


Fig. 6.1 **a** The most invasive genera, compiled from our list of 346 non-native and cryptogenic seaweeds. **b** Regions invaded by most different seaweed taxa [combining our bibliography with that of Williams and Smith (2007)]. The same taxa can invade multiple bioregions and the total number of cases in plot **b** therefore exceeds 346

6.3 How Non-native Seaweeds Get Around

Non-native seaweeds arrive into new regions through intentional or unintentional vectors. Intentional releases are few, perhaps <3 % of reported new incursions (Hewitt et al. 2007), and are mainly associated with aquaculture or, in rare instances, with scientific experimentation (Pickering et al. 2007). New intentional introductions could become even rarer in future because the public, managers, politicians and scientists have all become increasingly aware of the potential

impacts that might occur from intentional introductions. However, increased demand for food and seaweed-related products in a growing global population could supersede environmental concerns and lead to more introductions. Furthermore, some scientists advocate ‘assisted translocation’ (=‘intentional introduction’ in invasion research terminology) of species to new regions, to counter range contractions and extinctions in a warmer future (for discussions for and against, see Seddon 2010; Ricciardi and Simberloff 2009; Sandler 2010). Other researchers may focus on preserving and building ‘ecosystem services’ (Barbier et al. 2011) and therefore also suggest introductions to add or replace functional traits that are particularly valuable to humans, such as saltmarsh plants, mangroves and oysters that have been introduced to reduce erosion, build land and protect hinterland coastlines.

Most non-native seaweeds are, however, introduced accidentally rather than deliberately. The most important accidental vectors that have facilitated seaweed spread are the aquarium trade as ornamental plants, as ‘blind passengers’ associated with the intentional introductions, in ballast water and sea chests, attached to ship hulls, and infrastructure breaking down natural barriers such as canal building. Introductions associated with aquarium trade are particularly infamous due the release of *Caulerpa taxifolia* (M. Vahl) C. Agardh into the Mediterranean Sea (Meinesz 1999). However, the aquarium trade has become increasingly regulated with black-listed species, quarantine arrangements and stricter importation rules in many places (Hewitt et al. 2007; Padilla and Williams 2004). Still, non-native species are continually found in both commercial and personal aquaria and consequently pose a future invasion risk (Odom and Walters 2014; Williams et al. 2013). More seaweeds species (>25) have travelled through the Suez Canal, mainly from the Red Sea into the Mediterranean Sea (Williams and Smith 2007). However, there are few analogous marine examples around the world, suggesting that canal building, so far, has been a geographically isolated vector. Still, the future expansion of the Panama Canal could cause a similar spread of non-native species between Atlantic and Pacific bioregions (Ruiz et al. 2009).

Another vector is associated with ballast waters and sea chests (i.e. in waters and sediments held inside ships). Williams and Smith estimated about 25 known seaweed introductions through this vector, and although this vector is considered one of the most important for marine organisms generally, it is of comparatively little importance for seaweeds because of the adverse conditions for photosynthetic macrophytes (dark, nutrient poor, low water movements, high sediment loads) and because most seaweed propagules have relatively short lifespans (but see Flagella et al. (2007, 2010) for contrasting examples). Instead, ballast water is a much more important vector for invertebrates with pelagic larval stages, for sediment-associated fauna, for filter-feeding animals and for species with dormant resistant life stages such as many species of phytoplankton (Davidson and Simkanin 2012; Ibrahim and El-naggar 2012).

By far the most important vectors for seaweed introductions are associated with aquaculture, in particular shellfish transplants, and as hull-fouling organisms. Shellfish transplants have been particularly important in the past, with more than 70

species (mostly corticated rhodophyta) reported to be introduced by this vector (Mineur et al. 2007; Williams and Smith 2007). Oyster transplantations are likely responsible for several high-profile invasions, including those of *Sargassum muticum* (Yendo) Fensholt (Rueness 1989), *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Thomsen et al. 2006a) and *C. fragile* (Suringar) Hariot (Trowbridge 1998). However, methods now exist to kill epibiotic organisms, including seaweeds, while ensuring that the shellfish survive, for example by using short-term bleaching before seeding (Fitridge et al. 2012). Furthermore, increasing use of shellfish cultured in local, land-based facilities, could also lower the importance of this vector in future.

The final major vector is hull fouling, which is responsible for more than 70 seaweed introductions (Hewitt et al. 2007; Williams and Smith 2007; Mineur et al. 2008a). Hull fouling is a particularly important vector for filamentous species (Williams and Smith 2007), although larger species, including high-profile invaders such as *C. fragile* and *Undaria pinnatifida* (Harvey) Suringar likely also have been introduced to many places through hull fouling. Virtually, all seaweeds are capable of hull fouling but survival on ship hulls can be constrained by vessel speed, changes to environmental conditions throughout the voyage (such as changing salinity and temperature), low nutrient levels in offshore waters and the smooth surface of many hulls combined with toxic antifouling paints and coatings (Mineur et al. 2007). Increasing boat activity, both of commercial and recreational vessels, travelled over long or short distances, will likely continue to make this vector important in transporting seaweeds around the globe. Finally, we note that vectors for most non-native seaweeds are poorly described in the scientific literature and even for the better known case studies, described vectors are more like plausible guesses than based on rigorous tests and data (Williams and Smith 2007).

6.4 Success and Impacts of Non-native Seaweeds

After uptake, transport to and release into a new location, the success of a non-native seaweed is measured by how well it survives, grows and reproduces and whether it disperses and expands to nearby habitats, sites and regions. In these ‘invasion success’ studies, invader attributes are considered dependent variables, thereby contrasting with ‘invasion impact’ studies where invader attributes are independent variables. This distinction between success and impact is straightforward when interpreting data from manipulative studies but can be blurred for mensurative experiments where key attributes are beyond scientific control. For example, if mensurative data show a negative relationship between *Caulerpa* and seagrass abundances, this can occur because seagrass has a negative effect on *Caulerpa* (a success interpretation), because *Caulerpa* has a negative effect on seagrass (an impact interpretation), or because the relationship may be a spurious effect caused by a third unmeasured factor (Bulleri et al. 2010; Glasby 2012; Klein and Verlaque 2008; Ceccherelli and Campo 2002; Jaubert et al. 1999).

Success studies Success of an invasive seaweed depends on attributes related to the non-native seaweed and the invaded system (Catford et al. 2009). System attributes are typically subdivided into attributes related to abiotic conditions (e.g. salinity, temperature, hydrodynamic forces and desiccation), resources (e.g. space, light, nitrogen and phosphorous) and resident community structures (e.g. the identity and abundance of competitors, facilitators, grazers and other organisms). Many hypotheses have been proposed to explain the invasion success (or lack of) non-native species including seaweeds (Mitchell et al. 2006; Catford et al. 2009; Valentine et al. 2007; Alpert 2006). At least 19 ‘core’ hypotheses are commonly cited, which can be grouped into three clusters that highlight different aspects of invasion success. We use Catford et al.’s hypothesis nomenclature (cf. Table 3 in Catford et al. 2009) but excluded hypotheses that combined multiple core hypotheses (‘Darwin’s naturalisation’, ‘Global competition’, ‘resource-enemy release’, ‘indirect effects’, ‘opportunity windows’), that just rebranded other core hypotheses (‘adaptation’, ‘enemy reduction’) or that predicted success and failure at the same time and therefore are difficult to test (‘enemy inversion’, ‘dynamic equilibrium model’, ‘new associations’). We also added ‘facilitation- and habitat-cascades’ to the list (not included in Catford et al.’s review), because non-native seaweeds often are key players in these ecological interactions (Thomsen et al. 2010).

The first hypothesis cluster proposes that invasion success is determined by *attributes associated with the non-native seaweed*. This cluster includes the ‘ideal weed’ (Baker and Stebbens 1965), ‘propagule pressure’ (Lockwood et al. 2009) and ‘sampling’ (Crawley et al. 1999) hypotheses. The ideal weed hypothesis suggests that certain traits are universally important to successful invaders, particularly *r*-selected traits such as fast growth, high reproductive output and high dispersal capacity. However, there are few consistent patterns for the most successful invasive seaweeds, except perhaps for *U. pinnatifida* which has many weedy traits (Valentine et al. 2007). By comparison, propagule pressure and sampling hypotheses are ‘numbers game’ hypotheses that suggest that the more propagules (propagule pressure hypothesis, species traits are less important) or the more different species (sampling hypothesis, species traits are more important) that are introduced to a new region, the greater the chance that one of these propagules will establish a self-sustaining population (Britton-Simmons and Abbott 2008; Vaz-Pinto et al. 2012).

The second cluster emphasises that *attributes associated with the invaded system*, such as resource levels and local abiotic conditions, can explain invasion success. These core hypotheses highlight that high ‘fluctuating resource availability’ (Davis et al. 2000), high ‘environmental heterogeneity’ (Melbourne et al. 2007), medium-to-high ‘disturbances’ (Sher and Hyatt 1999), availability of ‘empty niches’ (Hierro et al. 2005) and low ‘habitat filtering’ (Procheş et al. 2008) all increase the likelihood that non-native species can establish populations following arrival. These hypotheses suggest that almost any non-native seaweed can be successful in systems that have a plethora of microhabitats, are heterogeneous, are frequently disturbed and have unused resources in space and time. Several of these

processes have been suggested to be important for high-profile seaweed invaders including *U. pinnatifida*, *S. muticum* and *Caulerpa racemosa* (Forsskål) J. Agardh (Valentine et al. 2007; Incera et al. 2010; Olabarria and Arenas 2014).

The final cluster emphasises that *biological interactions, in particular lack of co-evolution with local species*, can explain success of non-native species. In this cluster, ‘novel weapons’ (Callaway and Ridenour 2004), ‘enemy release’ (Keane and Crawley 2002), ‘evolution of increased competitive ability’ (Blossey and Notzold 1995), ‘enemy of my enemy’ (Eppinga et al. 2006), ‘limited similarity’ (Emery 2007), ‘specialist generalist’ (Sax et al. 2007), ‘invasional meltdown’ (Simberloff and Von Holle 1999) and ‘cascading habitat formation’ (Thomsen et al. 2010) highlight how non-native species become invasive, whereas ‘biotic resistance’ (Elton 1958), ‘missed mutualisms’ (Mitchell et al. 2006) and ‘increased susceptibility’ (Colautti et al. 2004) highlight why non-native species can fail to become invasive.

We are not aware of any research that has compared the relative merits of all these competing and overlapping core hypotheses for non-native seaweeds. However, we speculate that hypotheses assuming that seaweeds are limited by tight co-evolutionary processes at their place of origin (and lack of co-evolution at the new place) are *less* important for seaweeds, because seaweed–animal interactions are, compared to terrestrial systems, dominated by generalist-type interactions (Bell 1991; Enge et al. 2013; Hay and Steinberg 1992). Importantly, we hope future studies will test for interactions between multiple core hypotheses because we expect that many mechanisms exert selection pressure simultaneously and because mechanisms likely change during the life cycle of non-native seaweeds (Britton-Simmons 2006). For example, *U. pinnatifida* is well adapted to attach to ship hulls and spread in large numbers (~propagule pressure hypothesis) (Hay 1990) but has also many weedy traits, like fast growth and high reproductive output (~ideal weed hypothesis) (Dean and Hurd 2007; Schiel and Thompson 2012). *U. pinnatifida* is also successful in settling onto unoccupied microhabitat space and on biogenic substrata (~environmental heterogeneity hypothesis) (Schiel and Thompson 2012; Thompson and Schiel 2012), often becomes dominant following disturbances (~disturbance hypothesis) (Valentine and Johnson 2003, 2004) and is efficient in converting available resources into biomass (~fluctuating resource hypothesis) (Tait et al. 2015). Finally, *U. pinnatifida* is, of course, also constrained by physiological tolerance levels (~habitat-filtering hypothesis) (Morita et al. 2003; Peteiro and Sánchez 2012) even if *Undaria* colonises sites outside its native environmental range (James et al. 2014). In short, it is important that future studies test multiple core hypotheses simultaneously, rather than a single hypothesis at a time (Britton-Simmons 2006; Olabarria and Arenas 2014; Valentine et al. 2007; Williams and Smith 2007).

Impact studies In invasion impact studies, the non-native species is considered the causal agent of ecological change. Impact is therefore a synonym for ‘effect’, ‘consequence’ or ‘cause’. Impact studies focus on how invaders affect a particular property of a resident system, and the impact on this property can then be larger or smaller than a reference value (often the non-impacted reference value is defined as

zero). Impact can therefore be positive (>0), neutral (0) or negative (<0), which is a statistical measure that differs from the anthropocentric value judgement of whether an impact is 'good' or 'bad'. Impacts can be reported on cultural (economics, health, societal) or natural (biotic, abiotic) properties. Biotic properties can be divided into impacts reported on or above the species level; importantly, impacts reported above the species level can hide opposing effects if some species benefit and others are harmed. Invasion impacts, like successes, also depend on attributes of the non-native seaweeds and attributes associated with the biotic community, resource levels and abiotic conditions of the invaded system (Thomsen et al. 2011a). A highly cited impact formula suggests that the impact from a non-native seaweed is proportional to its abundance, its range (distribution) and its per capita effect (Parker et al. 1999), i.e. what it does to targeted response variables (in the context of its abundance and distribution). This framework highlights that processes which determine invasion success (cf. core hypotheses outlined in the previous section) also modify impact, partly by controlling the distribution and abundance of the non-native seaweed.

6.5 Common Types of Ecological Impacts

The impacts of invasive seaweeds have been reviewed in some detail (Williams 2007; Schaffelke and Hewitt 2007; Thomsen et al. 2009b; Williams and Smith 2007), concluding that impacts have been quantified from a fraction ($<10\%$) of known taxa, that impacts on native species can be strong and that underlying impact mechanisms are poorly known. Each of the 346 non-native and cryptogenic seaweeds have some level of impact on the invaded communities, contributing their biomass and adding new genotypes to the local species pools, modifying geochemical cycles through metabolic activities and by affecting other species in the community through ecological processes. However, impacts can be subtle or difficult to quantify, particularly if the non-native species is cryptic, if interactions with native species are few and weak, or, if strong interactions only occur in small areas, in short time windows, or in inaccessible habitats. Below we provide examples of ecological impacts grouped as 'negative' or 'positive', occurring through direct or indirect interactions (in indirect effects, an intermediate species is required for the impact to manifest).

Negative effects Many negative effects by non-native seaweeds occur through competition and habitat destruction (direct effects) or keystone competition and keystone habitat destruction (indirect effects). For example, non-native canopy-forming seaweeds, like *S. muticum*, *U. pinnatifida* and *C. fragile* sometimes have strong competitive effects on native seaweeds, competing for limiting resources such as nutrients, light and space (Staehr et al. 2000; Ambrose and Nelson 1982; Britton-Simmons 2004; Schmidt and Scheibling 2006; Levin et al. 2002; Casas et al. 2004). However, these negative effects appear to be weaker in intertidal

areas (Sánchez and Fernández 2005; Forrest and Taylor 2003; South et al. 2015; Olabarria et al. 2009), perhaps because desiccation and super-saturation of light are strong stressors here. Furthermore, some of these canopy-forming non-native seaweeds shed much of their thalli (*S. muticum* and *C. fragile*) or the entire thallus (*U. pinnatifida*) (Schiel and Thompson 2012; Wernberg et al. 2001), and effects associated with a canopy cover therefore could only occur seasonally (South et al. 2015). Similar mechanisms have been observed in soft-bottom systems where invasive *Caulerpa* species can compete with native seagrasses (Ceccherelli and Cinelli 1997; de Villele and Verlaque 1995), although other studies suggest that competition from *Caulerpa* is relatively small (Thomsen et al. 2012; Jaubert et al. 1999, 2003; Ceccherelli and Sechi 2002). Non-native seaweeds can also have negative effects on native organisms through modification or destruction of habitats, for example if they convert non-vegetated mud or sand habitats to vegetated meadows. Well-documented examples include *G. vermiculophylla* (Byers et al. 2012; Thomsen et al. 2007, 2010), *Caulerpa* species (Gribben and Wright 2006; Wright and Gribben 2008; Gribben et al. 2009b; McKinnon et al. 2009; Byers et al. 2010; Pacciardi et al. 2011), *S. muticum* (Strong et al. 2006), and invasive seagrasses (Willette and Ambrose 2009, 2012; Baldwin and Lovvorn 1994; Posey 1988; Berkenbusch et al. 2007; Ruesink et al. 2010) and salt marsh plants and mangroves (Demopoulos and Smith 2010; Thomsen et al. 2009a; Wu et al. 2009; Neira et al. 2007). In these examples, local species that depend on sand and mud, such as many infaunal species and burrowing fish, may be negatively affected by the non-native macrophytes (Wright et al. 2007; Gribben et al. 2009b; Tsai et al. 2010), although in some cases, these organisms can also survive under, around or on the macrophytes (Gribben and Wright 2006; Wright and Gribben 2008; Gribben et al. 2009b; McKinnon et al. 2009; Byers et al. 2010; Klein and Verlaque 2011).

Indirect negative effects from invasive seaweeds can occur through keystone competition where an invader reduces a resource that is important for other species within that community. For example, syngnathid and monacanthid fish were more abundant in native seagrass compared to invasive *Caulerpa* meadows (York et al. 2006), juvenile fish were more abundant in native seagrass beds than in the invasive seagrass *H. stipulacea* (Willette and Ambrose 2012) and gastropods and echinoderms were more abundant on native kelp compared to invasive *C. fragile* (Schmidt and Scheibling 2006). These fish, gastropods and echinoderms were probably less abundant around the non-native macrophytes (than around the native macrophytes), because these non-native species provide low-quality foraging grounds and poor protection against predators. In short, if these non-native macrophytes do indeed reduce the abundance of native seagrass and kelps, then they will have indirect negative effects on the same invertebrates and fish (=keystone competition).

Positive effects Invasive seaweeds can also have positive effects on local populations, directly through habitat formation and modification, and by being consumed by grazers, or indirectly through cascading habitat formation, consumption, competition or keystone consumption.

For example, seaweeds invading un-vegetated sediments provide habitat for epibenthic fauna (Thomsen and Wernberg 2015) that live among or on seaweeds, including *C. racemosa* (Klein and Verlaque 2011), *C. Taxifolia* (M. Vahl) C. Agardh (McKinnon et al. 2009) and *G. vermiculophylla* (Byers et al. 2012; Thomsen et al. 2010; Johnston and Lipcius 2012). Similar positive effects on fauna have also been shown for invasive seagrasses such as *H. decipiens* (Willette and Ambrose 2012) and *Z. japonica* Ascherson and Graebner in Engler (Berkenbusch and Rowden 2007; Berkenbusch et al. 2007; Posey 1988) when and where they colonise un-vegetated sediments. Many invasive seaweeds also add structure, biomass and productivity to vegetated rocky coasts (Thomsen et al. 2015). For example, the canopy-forming *S. muticum* and *C. fragile* provide additional habitat for epiphytic plants and invertebrates (Thomsen et al. 2006b; Jones and Thornber 2010; Schmidt and Scheibling 2006, 2007; Wernberg et al. 2004). Invasive seaweeds not only provide habitat, but can also be a food source, and indirectly fuel higher order consumers through trophic cascades. For example, juvenile invasive seaweeds (and seagrass) can provide a seasonal food supply (Sjotun et al. 2007; Thornber et al. 2004; Reynolds et al. 2012): *Littorina* Férussac snails consume *C. fragile* in tide pools (Scheibling et al. 2008), waterfowl graze invasive *Z. japonica* (Baldwin and Lovvorn 1994), and siphonalian seaweeds (*Codium* and *Caulerpa* spp.) are likely to have increased food availability for specialist saccoglossan grazers (Harris and Jones 2005; Trowbridge 2002; Trowbridge and Todd 2001). Still, most invasive seaweeds are not considered preferred food for native larger generalist grazers and smaller meso-grazers and many produce grazer-deterrent secondary metabolites, as shown for *S. muticum* (Britton-Simmons 2004; Engelen et al. 2011; Monteiro et al. 2009; Pedersen et al. 2005), *C. fragile* (Scheibling and Anthony 2001), *Caulerpa* species (Gollan and Wright 2006; Boudouresque et al. 1996), *G. vermiculophylla* (Nejrup and Pedersen 2010; Thomsen and McGlathery 2007; Nejrup et al. 2012; Rempt et al. 2012; Nylund et al. 2011) and *Lophocladia lallemantii* (Montagne) F. Schmitz and *Womersleyella setacea* (Hollenberg) R.E. Norris (Cebrian et al. 2011; Tomas et al. 2011a, b).

Invasive marine plants can also have positive indirect effects, for example through cascading habitat formation (Thomsen et al. 2010): invasive *S. muticum*, *C. fragile* and *G. vermiculophylla* provide primary habitat for sessile plants and animals, such as filamentous seaweeds and ascidians (Nyberg et al. 2009; Thomsen et al. 2006b, 2010; Engelen et al. 2013; Gestoso et al. 2012; Jones and Thornber 2010; Schmidt and Scheibling 2006, 2007; Wernberg et al. 2004). These epiphytic macro-organisms are likely to subsequently provide a secondary habitat for many other smaller organisms, such as hydrozoa, bryozoa and small mobile invertebrates. Invasive plants can also have indirect positive effects through cascading habitat modification. For example, *C. taxifolia* can reduce sediment redox potential, altering abiotic conditions and forcing infaunal bivalves to live at the sediment surface where they are exposed to sessile fouling organisms (Gribben et al. 2009a). Finally, positive effects of seaweed invasions can also be mediated through cascading consumption (trophic cascades), such as when invasive *C. fragile* is consumed by (invasive) *Littorina* snails (Scheibling et al. 2008), which are consumed

by (invasive) crabs (Eastwood et al. 2007; Trussell et al. 2002, 2004), which are consumed by native crabs, seabirds and fish (de Rivera et al. 2005).

6.6 Impacts Reviewed Across Studies, Seaweeds and Habitats

The many case studies about impacts from invasive seaweeds (cf. last section) have stimulated quantitative meta-analyses that aim to identify impact generalities across different non-native seaweed species, invaded communities and environmental conditions. In these studies, documented effects are standardised, typically with the Hedges d effect size or a log-response ratio (Borenstein et al. 2009), so that effects can be compared between studies. Here, we summarise the main finding from meta-analyses that have included non-native seaweeds as a test factor.

The first meta-analysis of seaweed invasion impacts reviewed field-based impact experiments and showed that invasive seaweeds generally had significant negative effects on local plant abundances, richness and diversity (Thomsen et al. 2009b). By contrast, there were no significant effects on seaweed ‘processes’ (e.g. growth, photosynthesis, respiration) or the abundance, richness and diversity of animal communities. However, the latter analysis was based on a small sample size and had large confidence limits. A follow-up analysis confirmed that non-native seaweeds, across the reviewed studies, have negative effects on diversity of native seaweeds (Thomsen et al. 2014). This study also tested whether trophic and functional ‘matching’ (i.e. pairing the trophic level or function of the invader *and* the impacted organism) could provide first-order predictions about impacts on diversity metrics. It was hypothesised that the net effect from non-native seaweeds on diversity would be negative within a trophic level but zero (or even positive) across trophic levels, based on the assumption that competition processes would dominate in the community within trophic levels (in plant–plant interactions) and habitat formation, habitat-modification and food-provisioning processes would dominate across trophic levels (in plant–animal interactions). The hypothesis was confirmed, showing negative effects of non-native seaweeds on the diversity of local seaweed communities, but with positive effects on local animal communities. Furthermore, a recent analysis reconfirmed that non-native seaweeds generally have negative effects on species within the same trophic levels (Maggi et al. 2015), although this study found no effects on species at higher trophic levels (effect size on animals was not statistically different from zero). The discrepancies between these meta-analyses (positive vs. no effect on animal communities) were likely due to there being different study-inclusion criteria. Maggi et al. (2015) included, in contrast to Thomsen et al. (2014), mensurative experiments, laboratory experiments and litter-bag experiments where the invader was dead and decomposing (Rodil et al. 2008; Taylor et al. 2010). These two analyses therefore highlight that readers

should be careful when extrapolating meta-analytical results beyond the domain of reviewed primary studies.

Three other meta-analyses have examined aspects of seaweed invasions. An analysis of seaweed impacts on seagrasses, measured in field and laboratory experiments, showed that non-native seaweeds have a less negative impact than native seaweeds (Thomsen et al. 2012). However, this analysis was confounded by the taxonomic status and attachment type of the non-native seaweeds, which were dominated by studies on *Caulerpa* species, a special group of clonal seaweeds attached with rhizomes to sediments. These types of non-native seaweeds have few documented cases of negative effects on seagrasses compared to many native seaweed taxa that are found in seagrass beds entangled around stems or epiphytic on leaves.

More recently, Tamburello et al. (2015) used a subset of the data analysed in Maggi et al. (2015), to test whether impacts co-vary with Halpern's (2008) 'global cumulative human impact index'. In other words, they tested whether seaweed invasion impacts increase or decrease with impacts from human activities (Halpern's index merges a range of human activities including pollution, fisheries, climate changes and eutrophication). This analysis showed that impacts from non-native seaweeds on community biomass and abundance become less negative or even neutral when moving from relatively pristine to heavily impacted environments (but the opposite trend was found on community 'evenness'). Thus, invasion impact appears to co-vary with other human stressors, being greater in stressed systems (presumably with lower resilience). Finally, Thomsen et al. (2015) conducted a meta-analysis to test whether invasion impacts on local plant communities differ when the invader itself was included as part of the total community. This analysis showed again that seaweed invaders have significant negative impacts on plant abundance and plant community richness, but also that these negative effects were cancelled out when the taxonomic status and abundance of the invader were included in the calculations of total community biomass and richness (i.e. the effect size was no longer significantly different from zero). Thus, non-native seaweeds appear, across species and invaded systems, to substitute, rather than increase or decrease, standing biomass and richness.

These meta-analyses all suggested that more impact studies are needed, especially on functional community responses, such as total system productivity, respiration, decomposition rates and nutrient uptake (Altieri et al. 2009; Green et al. 2012, 2013; Tait et al. 2015; Cacabelos et al. 2012; South et al. 2015). Furthermore, although the impact literature is extensive, the vast majority of case studies have tested for impacts of six high-profile invaders (*S. muticum*, *U. pinnatifida*, *C. taxifolia*, *C. racemosa*, *C. fragile* and *G. vermiculophylla*) likely biasing tests towards detecting strong impacts. It is critical that comprehensive impact analyses are conducted on more of the non-native seaweeds that have colonised coastlines around the world, to allow for better generalisations about seaweed invasions across habitats, bioregions and species assemblages.

6.7 New Meta-analysis; Impact Is Density-dependent and Non-native Seaweeds Affect Community Similarity

Two key aspects related to seaweed invasion impacts have not yet been tested with meta-analyses: density dependency and impacts on community structure measured by multivariate metrics. Below we address these research gaps.

6.7.1 *New Meta-analysis 1: Density-dependent Effects*

We tested whether impacts from non-native seaweeds are density dependent (density is defined loosely to include any abundance metric such as counts, length, coverage, biomass or volume); i.e. whether effects vary with the amount of an invasive seaweed found in a plot, site and region. We identified peer-reviewed papers describing manipulative field experiments in which invader abundance was controlled using addition or removal techniques with replicated treatments and controls. We included only experiments reporting impacts from at least three invasion densities (one of which could be a non-invaded control) so that paired effects within a study could be contrasted between low and high density treatments (Table 6.2).

We used Hedges effect size d , corrected for small sample sizes, to standardise effects between treatments, allowing us to include zero-value responses (Borenstein et al. 2009). An all-inclusive unbiased data selection criterion (Englund et al. 1999) was used to extract effect sizes for each paper, calculating d -values for *all* reported impacted resident organisms, test combinations (e.g. different depth levels Thomsen 2010) and quantified responses also on the same resident organism, such as seagrass leaf length, above ground biomass and below ground biomass (Drouin et al. 2012). One study presented data as x - y points on a graph of abundance of the seaweed versus fauna (because applied densities changed over time) (Byers et al. 2012). We extracted these x - y data and reclassified data into low (control), medium and high seaweed densities. To avoid problems associated with temporal autocorrelation, we included only the last data points from repeated measure experiments (Parker et al. 2006). Following the calculations of Hedges d between controls and invaded treatments, we calculated a ' Δd ' for each paired response (responses are paired because the same un-invaded control data are used to calculate d for both the low and high density treatments) (Thomsen et al. 2011b). If more than three invasion densities were tested, we contrasted only the effects between the lowest and highest densities. Nested and orthogonal experiments within research papers were treated as independent studies. Two tests examined whether effect sizes depended on the density of the non-native seaweeds. In the first, we examined whether paired d -values were different, using the formula $\Delta d = |d_{\text{high}} - d_{\text{low}}|$. In the second, more conservative, test, we examined whether the high density d was numerically larger

Table 6.2 Studies used in our meta-analyses

| Taxa | Data from figure | Reference |
|---|------------------|-------------------------------|
| <i>Caulerpa racemosa</i> (Forsskål) J. Agardh, <i>C. taxifolia</i> (M. Vahl) C. Agardh | 4 | Balata et al. (2004) |
| <i>Lophocladia lallemandii</i> (Montagne) F. Semitz | 3 | Bedini et al. (2014) |
| <i>Zostera japonica</i> Aschershon and Graebner | 2c–d | Berkenbusch and Rowden (2007) |
| <i>Zostera japonica</i> | 5b | Berkenbusch et al. (2007) |
| <i>Caulerpa racemosa</i> | 4 | Box et al. (2010) |
| <i>Sargassum muticum</i> (Yendo) Fensholt | 2 | Buschbaum et al. (2006) |
| <i>Gracilaria vermiculophylla</i> (Ohmi) Papenfuss | 4c, 5c, 6c | Byers et al. (2012)* |
| <i>Sargassum muticum</i> | 3a | Cacabelos et al. (2010) |
| <i>Codium fragile</i> (Suringar) Hariot | 3a–b, 4a–c | Drouin et al. (2012)* |
| Multiple (<i>Eucheuma denticulatum</i> (N.L. Burman F.S. Collins and Hervey + <i>Kappaphycus alvarezii</i>) | 4a–b | Eklöf et al. (2005) |
| <i>Caulerpa scalpeliformis</i> | 9 | Falcao and de Szechy (2005) |
| <i>Undaria pinnatifida</i> (Harvey) Suringar | 5 | Forrest and Taylor (2003) |
| Multiple (<i>Gracilaria salicornia</i> (C. Agardh) E.Y. Dawson + <i>Acanthophora spicifera</i> (M. Vahl) Børgesen) | 4 | Fukunaga et al. (2014) |
| <i>Caulerpa taxifolia</i> | 6a–b | Gallucci et al. (2012) |
| <i>Caulerpa racemosa</i> | 2 | Gennaro and Piazzi (2011) |
| <i>Sargassum muticum</i> | 2a, 4 | Gestoso et al. (2010) |
| <i>Caulerpa taxifolia</i> | 4 | Gribben et al. (2013) |
| <i>Asparagopsis armata</i> (Harvey) | 3 | Guerra-García et al. (2012) |
| <i>Gracilaria vermiculophylla</i> | 1–2 | Hamman et al. (2013)* |
| <i>Sargassum muticum</i> | 4a–c, 9a–c | Harries et al. (2007) |
| <i>Undaria pinnatifida</i> | Table 6.1 | Irigoyen et al. (2011) |

(continued)

Table 6.2 (continued)

| Taxa | Data from figure | Reference |
|---|------------------|-------------------------------|
| <i>Caulerpa racemosa</i> | 4 | Klein and Verlaque (2011) |
| <i>Sargassum muticum</i> | 3a, 3c | Lang and Buschbaum (2010) |
| <i>Sargassum muticum</i> | 4a–b, 5a–c | Lang and Buschbaum (2010)* |
| <i>Codium fragile</i> | 2a–c | Lutz et al. (2010) |
| <i>Caulerpa taxifolia</i> | 6a | Mateu-Vicens et al. (2010) |
| <i>Caulerpa taxifolia</i> | 2a–b | McKinnon et al. (2009) |
| Multiple (large group) | 3 | Mineur et al. (2008b) |
| <i>Sargassum muticum</i> | 3j | Olabarria et al. (2009) |
| <i>Caulerpa racemosa</i> | 2, 5 | Pacciardi et al. (2011) |
| <i>Caulerpa racemosa</i> , <i>Womersleyella setacea</i> (Hollenberg) R.E. Norris | 3 | Piazzì and Balata (2009) |
| <i>Caulerpa racemosa</i> | 2 | (Piazzì and Balata 2008) |
| <i>Caulerpa racemosa</i> , <i>C. taxifolia</i> , Multiple (<i>Acrothamnion preissii</i> (Sonder) E.M. Wollaston + <i>Womersleyella setacea</i>) | 4a–c | Piazzì and Cinelli (2003) |
| <i>Acrothamnion preissii</i> , <i>Womersleyella setacea</i> , Multiple (<i>Acrothamnion preissii</i> + <i>Womersleyella setacea</i>) | 5a–b | Piazzì et al. (2002) |
| <i>Caulerpa racemosa</i> , <i>C. taxifolia</i> , Multiple (<i>C. racemosa</i> + <i>C. taxifolia</i>) | 3 | Piazzì et al. (2003) |
| <i>Caulerpa racemosa</i> | 2 | Piazzì et al. (2005) |
| <i>Caulerpa racemosa</i> | 2 | Piazzì and Ceccherelli (2006) |
| <i>Sargassum muticum</i> | 2 | Sánchez et al. (2005) |
| <i>Sargassum muticum</i> | 6, 3a4, 3b4 | Sánchez and Fernández (2005) |
| <i>Codium fragile</i> | 5a–b | Schmidt and Scheibling (2006) |
| <i>Caulacanthus ustulatus</i> (Mertens ex Turner) Kützing | 1a, 1c, 1e, 2a–f | Smith et al. (2014) |
| <i>Undaria pinnatifida</i> | Raw data | South et al. (2015) |
| <i>Sargassum muticum</i> | 5b | Stæhr et al. (2000) |
| <i>Sargassum muticum</i> | 2a–b | Strong et al. (2006) |

(continued)

Table 6.2 (continued)

| Taxa | Data from figure | Reference |
|-----------------------------------|------------------|-------------------------------|
| <i>Gracilaria vermiculophylla</i> | Raw data | Thomsen and McGlathery (2006) |
| <i>Gracilaria vermiculophylla</i> | Raw data | Thomsen (2010) |
| <i>Gracilaria vermiculophylla</i> | 1a–h | Thomsen (2010)* |
| <i>Gracilaria vermiculophylla</i> | Raw data | Thomsen et al. (2010) |
| <i>Caulerpa racemosa</i> | 4 | Vázquez-Luis et al. (2012) |
| <i>Sargassum muticum</i> | 2a–d | Wernberg et al. (2004) |
| <i>Sargassum muticum</i> | 4 | White and Shurin (2011)* |
| <i>Caulerpa taxifolia</i> | 2a–d | York et al. (2006) |

References with asterisks were used for meta-analysis of density effects; all other references were used for meta-analysis of multivariate dispersion effects (i.e. showing MDS plots or where we have access to raw data). Note that multiple effect sizes could often be calculated from a single figure (e.g. as different MDI values for different sites)

than its paired low density d , using the formula $\Delta d = |d_{\text{high}}| - |d_{\text{low}}|$. Analysing numerical Δd -values is necessary to ensure that density-dependent facilitation is not cancelled out by density-dependent inhibition. Non-independent Δd -values from a study were averaged to produce independent Δd -values, using equal weight for each reported type of impact. Finally, un-weighted fixed effects analyses were made on the independent Δd -values in Metawin 2.1, to calculate $\Delta d_{\text{cumulative}}$ and 95 % bias-corrected confidence limits (CL) with 999 permutations (Rosenberg et al. 2000). $\Delta d_{\text{cumulative}}$ was interpreted to be significantly different from zero if the 95 % CL did not overlap zero.

In the first test, overall heterogeneity of effect sizes was small ($Q_{\text{total}} = 1.49$, $\text{df} = 9$, $p = 0.99$), indicating that effect sizes share a common value. The overall $\Delta d_{\text{cumulative}}$ was 0.61 and the 95 % bias-corrected confidence limits did not bracket zero (0.40–0.84) indicating that d_{high} was indeed *different* from d_{low} . In the second test, overall heterogeneity of effect sizes was again small ($Q_{\text{total}} = 1.29$, $\text{df} = 9$, $p = 0.99$). This $\Delta d_{\text{cumulative}}$ was slightly lower (0.52) and the 95 % bias-corrected confidence limits again did not bracket zero (0.31–0.74) highlighting that d_{high} had a *larger magnitude* than d_{low} . We conclude, therefore, based on the few studies that have tested for density-dependent effects, that seaweed invasion impacts, as a general rule, are density dependent. However, more studies are needed to enable specific analyses, for example, to identify non-linear density dependency, changes from positive to negative effect sizes, to locate thresholds and to make regression

models that can predict which non-native seaweeds have particular strong density-dependent impacts. This analysis also highlights that *all* seaweed invasion impact studies should report the abundance of the studied invader.

6.7.2 *New Meta-analysis 2: Effects on Community Structures*

Non-native seaweeds have strong effects on population abundances, growth, survival and community diversity and richness (all univariate metrics, see previous sections). However, non-native seaweeds can also affect multivariate community structure, often assessed through multivariate analysis of variance (Manova, Permanova) and multivariate regressions, and visualised on dimensional reduction methods such as principal coordinates analysis (PCA, PCO) or multidimensional scaling (MDS) (Viejo 1999; Staehr et al. 2000; Piazzi and Balata 2008). These methods typically test whether multivariate ‘centroids’ or ‘dispersion’ differ between invaded and non-invaded communities. The ‘centroid-analysis’ is non-directional in that it tests whether the ‘mean’ invaded community is different from the ‘mean’ non-invaded community. However, the ‘dispersion-analysis’ is directional, with several well-known examples suggesting that invaded communities are *less dispersed* in multivariate space (i.e. are more ‘homogenous’) than non-invaded communities (Staehr et al. 2000; Piazzi and Balata 2008). Unfortunately, invasion studies do not usually publish the entire species-sample data matrix or the associated sample similarity matrix from which multivariate dispersions can be calculated. Instead, multivariate invasion impact is typically visualised with 2D plots, where each x - y point represents a sample that can contain many species. The spatial distances between these sample points correlate with how similar the communities are, and invaded samples will be clustered compared to non-invaded samples if the invader increases community similarity in space (e.g. Fig. 2, Piazzi and Balata 2008) or over time (e.g. Fig. 5b, Staehr et al. 2000).

Here, we develop a method to test whether non-native seaweeds increase sample similarity across studies, by extracting x - y coordinates from published MDS plots. From these coordinates, sample matrices can be reconstructed, composed of two universal ‘pseudo-species’ from which the (imperfect) sample similarity matrices can be calculated. Reconstructed similarity matrices were then used to calculate Multivariate Dispersion Index values to test whether invasive seaweeds, across studies, increased between-sample similarities. These ‘MDI’ values have a minimum of -1 (dissimilarities among invaded samples are lower than any dissimilarities among non-invaded samples = non-native seaweeds ‘homogenise’ local communities) and a maximum of 1 (the opposite case = non-native seaweeds make local communities more heterogeneous (Warwick and Clarke 1993)).

We located peer-reviewed studies that compared samples from invaded and non-invaded communities in 2D MDS plots (Table 6.2) by searching Google Scholar and by back-tracking references in past reviews (Williams 2007; Thomsen et al. 2009b, 2011b, 2014; Schaffelke and Hewitt 2007; Maggi et al. 2015; Williams and Smith 2007). We included a few studies that did not show MDS plots for which we had access to raw data and therefore could calculate the sample similarity matrices (using common methods; Bray–Curtis similarity coefficient, square root transformed data and excluding the abundance of the invasive species) (Thomsen et al. 2010; Thomsen and McGlathery 2006; South et al. 2015). MDS plots were imported into TechDig and rescaled from 0 to 1 for the longest axis. Each sample was classified as invaded or non-invaded and its x – y coordinates extracted. A few samples overlapped on the plots, making it difficult to extract all samples (but >90 % of all samples were extracted from each plot). Extracted x – y coordinates represent the relative abundance of two ‘universal pseudo-species’ in the invaded versus non-invaded samples. Paired similarity matrices between the invaded and non-invaded samples were reconstructed from the two-species communities using Euclidean distances for untransformed data. This method provides a perfect spatial fit between the abundance of the pseudo-species and the published MDS plots they were derived from (see Fig. 6.2 for examples). For each plot, we also extracted data to test whether MDI values depended on whether (1) the impacted community was

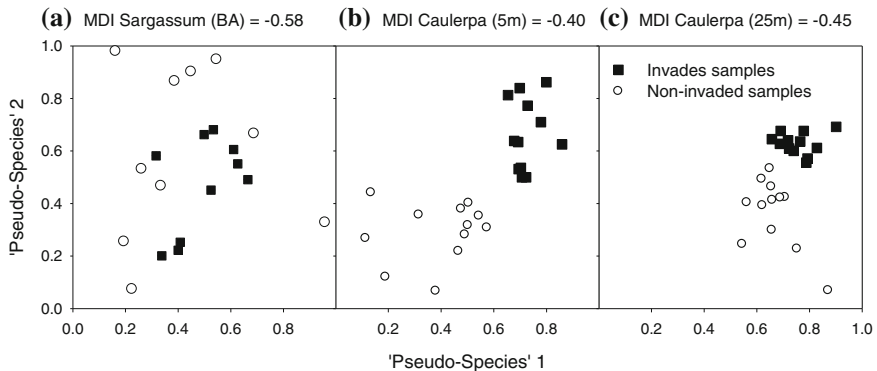


Fig. 6.2 Relative abundance of universal ‘pseudo-species’ 1 and 2 in invaded (*black squares*) and non-invaded (*white circles*) samples, reconstructed from two MDS plots; Fig. 5 in Staehr et al. (2000) and Fig. 2 in Piazzini and Balata (2008). The MDS plots were imported into TechDig and rescaled from 0 to 1 for the longest axis. Each sample was classified as invaded or non-invaded and its coordinates extracted (representing the relative abundance of universal ‘pseudo-species 1 and 2’). Similarity matrices were calculated for invaded and non-invaded samples using Euclidean distances based on the relative abundances of the two pseudo-species. Finally, MDI values were calculated for each set of paired similarity matrices (Warwick and Clarke 1993). The negative MDI values shown above each plot indicate invasion-driven ‘homogenisation’, i.e. invaded samples are spatially clustered both in time (a before vs. after invasion) and space (b at 5 m depth, c at 25 m depth)

composed of plants, animals or both (Thomsen et al. 2014), (2) the impacted community was composed of sessile, mobile organisms or both (Thomsen et al. 2014), (3) the field method was based on a manipulative or mensurative experiment (Maggi et al. 2015) and (4) analysis included (Staeher et al. 2000; Klein and Verlaque 2011) or excluded (Balata et al. 2004) the abundance of the invader in the similarity matrix. We finally calculated a MDI value for each reconstructed paired invaded versus non-invaded similarity matrix (Warwick and Clarke 1993).

Meta-analytical methods followed the previous density analysis; factorial and nested experiments were treated as independent data, as were effects from the same invasive species reported in different studies. Only the last data point was used from repeated measure data and only effects that compared the highest invader density to non-invaded samples were used from multidensity experiments. Invasion effects reported on different communities within a single study (e.g. on endobenthic and epibenthic communities, Lang and Buschbaum 2010) were also treated as independent effects. Cumulative effect sizes ($MDI_{\text{cumulative}}$) with 95 % bias-corrected CL were calculated in Metawin 2.1 with 999 permutations (Rosenberg et al. 2000). $MDI_{\text{cumulative}}$ was interpreted to be significantly different from zero or another $MDI_{\text{cumulative}}$ if the 95 % CL did not overlap zero or each other, respectively.

We found no significant effects, i.e. treatments were not significantly different from zero or each other (Fig. 6.3a–d). Still, there were several interesting (non-significant) trends, indicating that effect sizes were larger and more negative *within* rather than *between* trophic or functional groups (Fig. 6.3a, b). Perhaps with more studies, and smaller confidence limits, it will become clearer whether non-native seaweeds, as a general rule, homogenise ‘similar’ invaded plant communities but not ‘different’ invaded animal communities. Our results also highlight that conclusions based on a few well-cited studies (Staeher et al. 2000; Piazzini and Balata 2008) should only cautiously be interpreted out of the context of the methods, invasive species, invaded community and surrounding abiotic environment. We expect analogous multivariate directional tests in future will have stronger predictive power, when (1) more studies report impacts on different types of communities, (2) more test factors and levels within factors are included in tests (e.g. on form-groups such as epiphytes, canopies and understory communities) and (3) tests also include interactions between factors (e.g. between form-groups and field and data collection methods). Finally, future studies should also test how robust our ‘dispersion meta-analysis’ is by modelling how much dispersion values can vary in direction and magnitude depending on MDS stress values, chosen dispersion index (e.g. Permdisp vs. MDI), plot type (e.g. PCO vs. MDS), distance metric (e.g. Bray–Curtis vs. Gower), measurements variables (e.g. cover vs. biomass data) and transformation methods (e.g. untransformed vs. log-transformed).

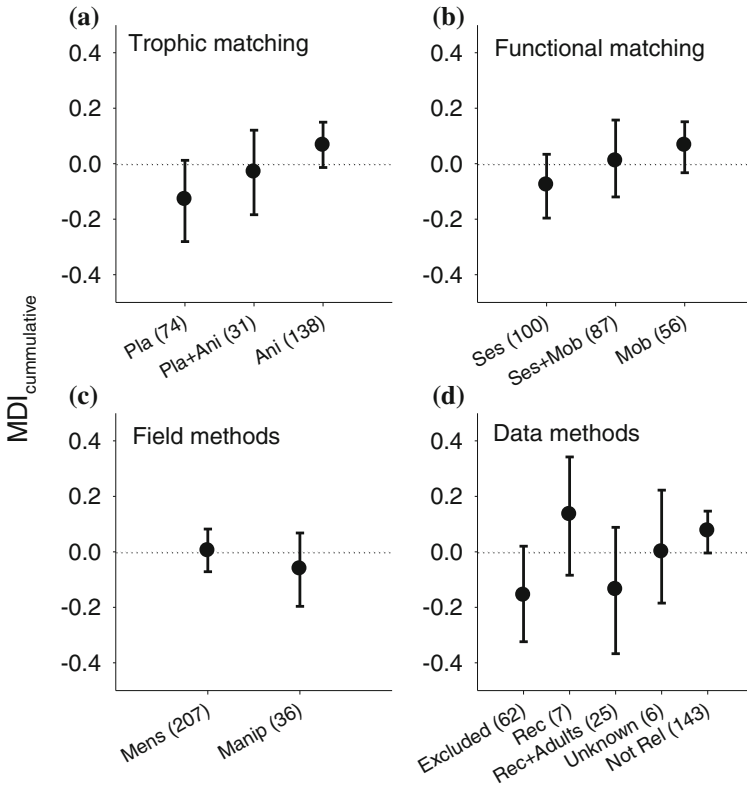


Fig. 6.3 Meta-analysis of 243 MDI values extracted from MDS plots that contrast invaded and non-invaded community samples. Negative values correspond to samples being more similar ('homogenisation') and numbers in brackets correspond to replication levels. Impacts of invasive seaweeds were evaluated on (a) plant (*Pla*), animal (*Ani*) or combined (*Pla* + *Ani*) communities, (b) sessile (*Ses*), mobile (*Mob*) or combined (*Ses* + *Mob*) communities, (c) communities measured in mensurative (*Mens*) or manipulative (*Manip*) field experiments and (d) communities where the invader itself was included or excluded. For plot d, MDI values were calculated for 5 types of reported similarity matrices; (1) excluding the invader (*Excluded*), (2) including the invader's new recruits (*Rec*), (3) including both the new recruits and the abundance of the invader itself (*Rec* + *Adult*), (4) studies where it could not be determined (*Unknown*) and (5) irrelevant studies (*Not Rel*), i.e. where the invaded community is different from the invasive species (here animal communities)

6.8 Summary

We conducted a bibliographic survey, adding 69 taxa to a published list of 277 seaweeds, thereby updating the total worldwide list of non-native and cryptogenic seaweeds to 346. None of these new non-native seaweeds have received much scientific scrutiny, but several may over time become abundant in invaded regions.

The seaweed genera with most non-native taxa are *Polysiphonia*, *Hypnea*, *Codium*, *Gracilaria* and *Caulerpa*. Bioregions that have received most non-native seaweeds are the Mediterranean Sea, followed by NE Atlantic, Australasia, NE Pacific and the NW Atlantic. Our tally is most likely an underestimate because (1) seaweeds may have been introduced to new regions prior to modern science, (2) morphologically similar non-native and native species may co-occur and remain taxonomically cryptic, (3) under-studied regions can include non-native taxa that are (4) poorly described, (5) difficult to identify, (6) rare or (7) have invaded inaccessible areas and habitats. The most important vectors that carry seaweeds around the world are hull fouling and as ‘blind passengers’ associated with aquaculture (in particular seaweeds attached to shell transplants), together accounting for >75 % of known seaweed introductions. These vectors are likely to continue to spread seaweeds around the world.

Once a non-native seaweed has arrived in a new location, it can establish a permanent population, spread (secondarily) through natural dispersal or associated with human vectors, increase in abundance and affect local species and ecosystem properties. Establishment, increase in abundances and secondary spread is quantified in ‘success studies’, whereas the effects on the invaded communities are quantified in ‘impact studies’. The success of non-native seaweeds depends on attributes of the non-native seaweeds and attributes associated with the invaded system, including the biotic community, resource levels and abiotic conditions. Many ‘core hypotheses’ have been suggested to explain why some non-native species (seaweeds included) become invasive or fail, of which the ‘ideal weed’, ‘propagule pressure’, ‘sampling’, ‘fluctuating resource availability’, ‘environmental heterogeneity’, ‘disturbances’, ‘empty niches’, ‘habitat filtering’, ‘limited similarity’ and ‘specialist-generalist matching’ are important to understand. Impact framework also suggests the direction and magnitude of impacts depends on attributes of the non-native seaweeds and attributes associated with the biotic community, resource levels and abiotic conditions of the invaded system. Thus, any process that increases success (cf. core hypotheses outlined above) should modify impact, by controlling the distribution and abundance of the non-native seaweed. Impacts can, like success, be difficult to quantify, if the non-native seaweed is inconspicuous or difficult to identify or find, if interactions with native species are few and weak, or if strong interactions occur only in small areas, short time windows and in inaccessible habitats. Case studies have shown that many negative effects by non-native seaweeds occur through competition and habitat destruction (direct effects) or keystone competition and keystone habitat destruction (indirect effects). However, invasive seaweeds can also have positive effects on local populations, directly through habitat formation and modification and by being consumed, or indirectly through cascading habitat formation, consumption, competition or keystone consumption.

Case studies documenting seaweed invasion impacts have stimulated meta-analytical synthesis that aims to identify impact generalities across different invasive seaweeds, invaded communities and environmental conditions. Meta-analyses have shown that invasive seaweeds typically have a negative effect

on local plant abundances, richness and diversity but positive or neutral effects on animal communities. Furthermore, negative effects reported on local plants can become less negative or neutral when moving from pristine to heavily human-impacted environments. Finally, our new meta-analyses presented in this chapter indicate that impacts increase with the abundance of non-native seaweeds and that non-native seaweeds may increase sample similarity in invaded plant communities, but not in animal communities (but these findings were based on a non-significant trend). Although the impact literature is extensive, most studies have tested for impacts of only 6 high-profile invaders (*S. muticum*, *U. pinnatifida*, *C. taxifolia*, *C. racemosa*, *C. fragile* and *G. vermiculophylla*). It is therefore important that similar comprehensive analyses are conducted on non-native seaweeds to allow for better generalisations and predictions about seaweed invasion impacts.

In conclusion, at least 346 non-native and cryptogenic seaweeds have altered local shallow water coastal communities in most major biogeographical regions around the world, and this pattern is likely to increase as human populations, transport and other co-occurring stressors continue to increase.

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