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Assessing the impacts of nonindigenous marine macroalgae: an update of current knowledge

Abstract: Nonindigenous marine species continue to be one of the foremost threats to marine biodiversity. As an update to a 2007 review of the impacts of introduced macroalgae, we assessed 142 additional publications to describe species' impacts as well as to appraise information on the mechanisms of impact. Only 10% of the currently known nonindigenous macroalgal species were subjects of ecological impact studies, with changed community composition as the most commonly reported effect. Economic impacts were rarely published. Recent research has focused on the impacts of introduced macroalgal assemblages: red algal introductions to the Hawaiian Islands and turf algae in the Mediterranean. Several general issues were apparent. First, many publications included nonsignificant results of statistical analyses but did not report associated power. As many of the studies also had low effect and sample size, the potential for type II errors is considerable. Second, there was no widely accepted framework to categorize and compare impacts between studies. Information in this updated review was still too sparse to identify general patterns and mechanisms of impact. This is a critical knowledge gap as rates of introductions and hence impacts of nonindigenous macroalgae are expected to accelerate with climate change and increasing global trade connectivity.

Keywords: biosecurity; ecological impacts; economic impacts; global change; introduced species; macroalgae.

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Introduction

The threat to global marine biodiversity and resources of the world's oceans by anthropogenic influences is widely acknowledged. In particular, overfishing, habitat alteration and destruction, pollution, global climate change, and the introduction of nonindigenous marine species (NIMS) are the identified key pressures, especially in coastal regions (Vitousek et al. 1997, Carlton 2000, Millennium Ecosystem Assessment 2005, Halpern et al. 2008, Micheli et al. 2013). Introductions of marine species continue to increase globally, with the invasion rate accelerations during the last 30 years attributed to increased global trade and changes in trade patterns resulting from vector management (Ruiz et al. 2000, Perrings et al. 2002, Ribera Siguan 2002, Costello and Solow 2003, Hewitt 2003, Campbell et al. 2007).

It is widely recognized that the impacts of marine introductions remain poorly understood (Ruiz et al. 1999, Grosholz et al. 2000, Grosholz 2002, Molnar et al. 2008) and represent one of the critical knowledge gaps in developing risk-based biosecurity strategies (Ruiz and Carlton 2003, Hewitt et al. 2004a, Davidson et al. 2013, Azmi et al. 2015, Blackburn et al. 2014, Davidson and Hewitt 2014). Impacts are documented in fewer than 30% of globally recognized NIMS, with even fewer impacts quantitatively assessed (Hewitt et al. 2011b). Despite this, it is increasingly argued that rather than attempting to manage species on the basis of their evolutionary origins alone, we should focus on the management and intervention of only those species that cause impact (e.g., Davis et al. 2011, Kumschick et al. 2015).

Marine macroalgae are a significant component of NIMS (Schaffelke et al. 2006, Hewitt et al. 2011b), with current global estimates of introduced macroalgae ranging from 163 (Ribera Siguan 2002) to >300 species (Azmi 2010, Azmi et al. 2015, Hewitt et al. unpublished data). However, studies of introduced macroalgal impacts on environmental, economic, or sociocultural values are documented for <20% of recognized introductions and only 9% of environmental/ecological impacts (Azmi 2010, Hewitt et al. unpublished data).

Several reviews attempt to evaluate the impacts of introduced marine macroalgae (e.g., Schaffelke and

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Hewitt 2007, Williams and Smith 2007). Impacts of introduced macroalgae are mostly documented from a few, well-studied, high-profile species (e.g., *Caulerpa cylindracea* [previously *Caulerpa racemosa* var. *cylindracea*; Belton et al. 2014], *Caulerpa taxifolia*, *Codium fragile* ssp. *tomentosoides*, *Sargassum muticum*, and *Undaria pinnatifida*; e.g., Gollan and Wright 2006, Scheibling and Gagnon 2006, Raffo et al. 2009, Bulleri et al. 2010, White and Shurin 2011).

This review is an update of an earlier review on the impacts of nonindigenous macroalgae (Schaffelke and Hewitt 2007). In this update, we identify and evaluate new information and review the state of knowledge of macroalgal introductions and their associated impacts. Our aims were to find patterns of impacts, to examine whether certain species are more likely to cause significant impacts, and to identify mechanisms contributing to the observed impacts. In addition, we evaluate if and how the recommendations of the original review have been implemented.

We categorize reported impacts and classify the type of the information (e.g., observations from surveys, data from manipulative field experiments). Given the complexity of community and ecosystem interactions and the difficulty of assessing whether a given change is “positive” or “negative”, we include all significant effects.

Materials and methods

This review is based on papers reported in Web of Science and Google Scholar databases published between 2005 and 2014 (the period subsequent to that considered by Schaffelke and Hewitt 2007) using the following search terms: “macroalg* OR seaweed OR marine plant” AND “impact” AND “invasive OR nonindigenous OR introduced”. We found 264 publications in Web of Science and 23,200 in Google Scholar; we discarded irrelevant publications, reviews, and publications offering only distributional or observational data, leaving 142 papers (135 reporting ecological impacts, 6 reporting economic and societal impacts, and 1 reporting both ecological and economic/societal impacts). Seventeen publications reported ecological impacts from several introduced species. We considered each species as a separate case study, unless the study explicitly addressed interactions between species; this resulted in a total number of 158 published case studies. We note that studies which fail to recognize or articulate that the subject is nonindigenous will not be captured by these search terms.

Various categorizations of impact (or consequence) have been suggested (e.g., Parker et al. 1999, Campbell 2008, 2011, Campbell and Hewitt 2011, Blackburn et al. 2014, Ojaveer et al. 2015). For this review, we followed the categories of Schaffelke and Hewitt (2007) to identify and group potential mechanisms of direct or indirect impact.

Ecological and evolutionary impacts:

- Direct and indirect competition with native biota (e.g., for light or substratum)
- Space monopolization
- Change in community composition
- Effects on higher trophic levels (e.g., herbivores, associated fauna, and toxicity)
- Habitat change (e.g., changed structure, sediment accumulation)
- Change of ecosystem processes (e.g., alteration of trophic structure)
- Genetic effects:
  - Within a species (e.g., introgression)
  - Between species (e.g., hybridization)

Economic and societal impacts:

- Direct
  - Costs of loss of ecosystem functions or values
  - Impacts on environmental amenity
  - Impacts on human health
- Indirect
  - Management costs (government/nongovernment)
  - Costs of research into introduced species
  - Costs for eradication and control measures
  - Costs for education/ extension campaigns.

Results

The 158 published case studies (with an additional two economic impacts described from personal communication) reported ecological and economic impacts for 30 species of introduced macroalgae (Tables 1–3, Figures 1–4).

Table 1: Summary of macroalgae and publications (by macroalgal type) included in review of ecological impacts. Publications (by macroalgal type) will not sum to 136 as 17 included multiple species.

Component	Total (% of total)
Number of species	30
Green (Chlorophyta)	9 (30%)
Red (Rhodophyta)	17 (57%)
Brown (Phaeophyceae)	4 (13%)
Number of publications	136
Green (Chlorophyta)	70 (47%)
Red (Rhodophyta)	61 (35%)
Brown (Phaeophyceae)	26 (18%)

Table 2: Summary information of case studies of impacts of nonindigenous macroalgae. (NOTE: Legends for Method and Effect are below the table).

Species	Method	Effect	Location	References
Acanthophora spicifera (M. Vahl) Børgesen (R)				
	Sur	SM	USA (Hawaii)	Lapointe and Bedford 2011
	O	CC	Marshall Islands	Tsuda et al. 2008
	O	SM	Hawaii	Weijerman et al. 2008
	Sur	–	Mexico	Avila et al. 2012
Asparagopsis armata Harvey[a](R)				
	Sur (comp)	CC	Iberian Peninsula (Spain and Portugal)	Guerra-Garcia et al. 2012
	Sur	–	Mediterranean	Pacios et al. 2011
Avrainvillea amadelpha (Montagne) A. Gepp *et* E.S. Gepp (G)				
	Sur (comp), E	CC	Hawaii	Longenecker et al. 2011
	Sur (comp), E	HC	Hawaii	Martinez et al. 2009
Bonnemaisonia hamifera Hariot (R)				
	Lab, E	TO	Sweden	Enge et al. 2012
	Lab	HT	Sweden	Enge et al. 2013
Caulacanthus ustulatus (Mertens *ex* Turner) Kutzing (R)[a]				
	Sur (comp)	CC	California	Smith et al. 2014
Caulerpa brachypus f. *parvifolia* (Harvey) A.B. Cribb[a] (G)				
	Sur	SM	Florida	Lapointe and Bedford 2010
Caulerpa cylindracea (Sonder) (G)				
	Sur (comp)	CC	Adriatic Sea	Antolic et al. 2008
	Sur (BACI)	CC	Ionian Sea (Italy)	Baldacconi and Corriero 2009
	Sur (comp)	SM	W Mediterranean	Box et al. 2010
	E	HC	Mediterranean (Italy)	Bulleri et al. 2010
	E	SM	Mediterranean (Italy)	Gennaro and Piazzi 2011
	Sur (comp)	CC	NW Mediterranean	Klein and Verlaque 2009
	E	CC	Mediterranean (France)	Klein and Verlaque 2011
	O	SM	Adriatic Sea (Croatia)	Kružić et al. 2008
	Sur (comp)	CC	Italy	Lorenti et al. 2011
	Sur	SM	Italy	Montefalcone et al. 2007b
	Sur (comp)	CC	Italy	Piazza and Balata 2008
	E, Sur (comp)	CC	NW Mediterranean	Piazzi and Ceccherelli 2006
	E	HC	Italy	Piazzi et al. 2005
	Sur (comp)	SM	Italy	Piazzi et al. 2007a
	Lab	TO	Italy	Raniello et al. 2007
	Sur, Lab	TO	Italy	Terlizzi et al. 2011
	O	SM	Croatia	Zuljevic et al. 2011
	Sur (comp)	CC, HC	Spain	Vazquez-Luis et al. 2008 Vazquez-Luis et al. 2009
	Sur (comp)	CC, HT	Mediterranean	Deudero et al. 2011
	Sur (comp)	TO	Mediterranean	Gorbi et al. 2014
	Sur (comp)	TO	Mediterranean	Felline et al. 2014
	Sur (comp)	HC	Mediterranean	Matijevic et al. 2013
	Sur (comp)	HT	Spain	Vazquez-Luis et al. 2013
	E, Sur (comp)	HC, CC	NW Mediterranean (Italy)	Pacciardi et al. 2011
Caulerpa prolifera (Forsskål) J.V. Lamouroux[a] (G)				
	E	SM	Florida	Taplin et al. 2005
Caulerpa scalpelliformis (R. Brown *ex* Turner) C. Agardh[a] (G)				
	O, Sur (comp)	SM, CC	Brazil	Falcao and de Szechy 2005
Caulerpa taxifolia (M.Vahl) C. Agardh (G)				
	Lab	HT	Australia	Burfeind et al. 2009
	Sur (comp)	CC	Australia	Galluci et al. 2012
	Sur, E, Lab	CC, HT	Australia	Gollan and Wright 2006
	Sur (comp), E	HT	Australia	Gribben et al. 2009

(Table 2: Continued)

Species	Method	Effect	Location	References
	Sur (comp), Lab	HT	Australia	Gribben and Wright 2006
	Sur (comp)	HT	France	Longepierre et al. 2005
	Sur (comp)	CC	Australia	McKinnon et al. 2009
	E	HC, CC	Australia	Taylor et al. 2010
	Sur (comp)	HT	Australia	York et al. 2006
	E	CC	Australia	Bishop and Kelaher 2013
	Sur, E	CC	Australia	Gribben et al. 2013
	O, E	–	Australia	Glasby 2013
	E	G	Australia	Wright et al. 2012
Chara connivens P. Salzmann *ex* A. Braun[a] (G)				
	E	HT	Baltic Sea	Kotta et al. 2004
Codium fragile ssp. *tomentosoides* (van Goor) P.C. Silva (G)				
	Sur (comp), E	HT	Adriatic Sea	Bulleri et al. 2006
	E, Sur (comp)	SM	Eastern Canada	Drouin et al. 2012
	Sur	CC	Maine	Harris and Jones 2005
	Sur (comp)	CC	Nova Scotia	Kelly et al. 2011
	Lab	TO	Nova Scotia	Lyons et al. 2007
	E	SM	Nova Scotia	Scheibling and Gagnon 2006
	Sur (comp)	CC	Nova Scotia	Schmidt and Scheibling 2006
	E	CC	Nova Scotia	Schmidt and Scheibling 2007
	E	–	New York	Carroll and Peterson 2013
Eucheuma denticulatum (N.L. Burman) F.S. Collins *et* Hervey[a] (R)				
	Lab	?	Tanzania	Mtolera et al. 1996
Fucus evancescens C. Agardh (B)				
	Lab	TO	Sweden	Forslund et al. 2010
	Lab, Sur (comp)	TO, CC	Sweden	Wikström et al. 2006
Fucus serratus Linnaeus[a] (B)				
	O, Lab	SM, G	Eastern Canada	Johnson et al. 2012
Gracilariopsis spp. (R)				
	E	SM	California, USA	Huntington and Boyer 2008
Gracilaria salicornia (C. Agardh) E.Y. Dawson (R)				
	Sur (comp)	HC	Hawaii	Martinez et al. 2012
Grateloupia turuturu Yamada[a] (R)				
	Sur (comp)	CC, HT	Long Island Sound	Janiak and Whitlatch 2012
Gracilaria vermiculophylla (Ohmi) Papenfuss[a] (R)				
	Sur	SM	Portugal	Abreu et al. 2011
	Lab	–	Denmark	Höffle et al. 2011
	Lab	SM	Denmark	Martinez-Luscher and Holmer 2010
	Sur	HC, CC	Virginia	Thomsen et al. 2009
	Lab	HT	Baltic Sea	Weinberger et al. 2008
	E	SM, CC	Denmark	Thomsen et al. 2013
	E, Sur	CC	Georgia, South Carolina	Byers et al. 2012
	E	SM	Baltic Sea	Hammann et al. 2013
	Sur (comp)	HT	Portugal	Cacabelos et al. 2012
	E	HT, HC	Georgia	Wright et al. 2014
	Sur	CC	Virginia, Sweden	Nyberg et al. 2009
Kappaphycus spp. (R)				
	Sur	SM	Fiji	Ask et al. 2003
	Sur	SM	India	Chandrasekaran et al. 2008
	Sur	SM	Hawaii	Conklin and Smith 2005

(Table 2: Continued)

Species	Method	Effect	Location	References
	O	SM	India	Kamalakannan et al. 2010
	E, Sur (comp)	SM	India	Kamalakannan et al. 2014
Lophocladia lallemandii (Montagne) F. Schmitz[a] (R)				
	Sur (comp)	HT	Mediterranean	Ballesteros et al. 2007
	Sur (comp)	HT	Mediterranean	Box et al. 2009
	Lab, Sur (comp)	HT	Mediterranean	Cabanellas-Reboredo et al. 2010
	Sur (comp)	HC	Mediterranean	Deudero et al. 2010
	Sur (comp)	TO	Mediterranean	Sureda et al. 2008
	Sur (comp)	CC	Mediterranean	Bedini et al. 2014
	Sur (comp)	TO	Mediterranean	Tejada and Sureda 2014
	Sur	SM	Mediterranean	Marba et al. 2014
Neosiphonia harveyii (Bailey) M.-S. Kim, H.-G. Choi, Guiry *et* G.W. Saunders (R)				
	E, Lab	–	Rhode Island	Rohr et al. 2011
Sargassum muticum (Yendo) Fensholt (B)				
	Sur (comp)	CC	North Sea	Buschbaum et al. 2006
	Sur (comp)	CC	Spain	Gestoso et al. 2012
	E	SM	North Sea	Lang and Buschbaum 2010
	Lab	HT	Portugal	Monteiro et al. 2009
	E	SM	Spain	Olabarria et al. 2009
	Sur (comp)	HC	Denmark	Pedersen et al. 2005
	E	CC	Spain	Rodil et al. 2008
	E	–	Spain	Sánchez and Fernández 2005
	E	–	United Kingdom	Strong and Dring 2011
	Sur (comp)	CC	United Kingdom	Strong et al. 2006
	O	SM	Denmark	Thomsen et al. 2006
	E	SM, CC	Vancouver	White and Shurin 2011
	Sur (comp), Lab	HT	Washington, USA	Britton-Simmons et al. 2011
	Sur (comp)	CC	Portugal	Engelen et al. 2013
	Sur (comp)	CC	Spain	Gestoso et al. 2010
	Sur (comp)	CC	Spain	Gestoso et al. 2012
	E	CC, HT	Ireland	Salvaterra et al. 2013
	Lab	HT	Portugal	Vaz-Pinto et al. 2014
Undaria pinnatifida (Harvey) Suringar (B)				
	E	–	United Kingdom	Farrell and Fletcher 2006
	E	CC	Patagonia	Irigoyen et al. 2011a
	Sur (comp)	CC	Argentina	Raffo et al. 2009
	Sur (comp)	HT	Patagonia	Irigoyen et al. 2011b
	E	SM	Australia	Carnell and Keough 2014
Womersleyella setacea (Hollenberg) R.E. Norris (R)				
	Sur (comp)	CC	Mediterranean	Antoniadou and Chintiroglou 2007
	O	SM	Mediterranean	Batelli et al. 2008
	Sur (comp)	SM	Mediterranean	de Caralt and Cebrian 2013
Combinations				
Ceramium rubrum C. Agardh[a] (R), *Chaetomorpha linum* (O.F. Müller) Kützing[a] (G)	Lab	TO	Denmark	Holmer and Nielsen 2007
C. cylindracea (G), *C. taxifolia* (G)	Sur (comp)	HC, TO	Western Mediterranean	Holmer et al. 2009
C. fragile (G), *G. turuturu* (R)	Sur (comp)	CC, HC	Rhode Island	Jones and Thornber 2010
C. taxifolia, C. cylindracea (G)	Sur	SM	Italy	Montefalcone et al. 2010
H. musciformis, A. spicifera (R)	E	HT	Hawaii, Caribbean	Vermeij et al. 2009
H. musciformis, A. spicifera, G. salicornia (R)	O	TO	Hawaii	Van Houtan et al. 2010

(Table 2: Continued)

Species	Method	Effect	Location	References
C. cylindracea (G), *L. lallemandii* (R), *W. setacea* (R), *Acrothamnion preissii* (Sonder) E.M Wollaston (R)	E	HT	Mediterranean	Tomas et al. 2011
C. cylindracea (G), *W. setacea* (R)	Sur (comp)	CC, SM	Mediterranean	Piazzi et al. 2007b
C. cylindracea, C. taxifolia (G)	Sur	SM	Italy	Montefalcone et al. 2007a
C. scalpelliformis, C. taxifolia, C. filiformis (G)	Lab, E	HT	Australia	Davis et al. 2005
W. setacea, A. preissii (R)	Sur, E	CC	Mediterranean	Linares et al. 2012
C. cylindracea (G), *W. setacea* (R)	Sur (comp)	CC	Mediterranean	Piazzi and Balata 2009
C. cylindracea (G), *W. setacea* (R)	E	SM	Mediterranean	Cebrian et al. 2012
G. salicornia (R), *A. specifera* (R)	Sur (comp)	CC	Hawaii	Fukunaga et al. 2014
C. cylindracea (G), *C. taxifolia* (G)	Sur (comp)	CC, HT	Mediterranean	Deudero et al. 2014
L. lallemandii (R), *C. cylindracea* (G)	Sur (comp)	–	Mediterranean	Kersting et al. 2014
Heterosiphonia japonica (R)[a], *B. hamifera* (R)	Lab	HT	Sweden	Sagerman et al. 2014

B, brown algae (Phaeophyceae); G, green algae (Chlorophyta); and R, red algae (Rhodophyta). Method: Sur, field survey; Sur (comp), field survey comparing invaded and noninvaded sites; Sur (BACI), field survey with temporal comparisons before/after invasion; E, field experiment; Lab, laboratory experiment or assay; and O, observational study. Effect: SM, space monopolization; CC, change in community composition; G, genetic effects; HT, effects on higher trophic levels; TO, toxicity; HC, habitat change.

[a] Species not found in Schaffelke and Hewitt (2007) review.

Ecological impacts

Our evaluation confirmed that the predominant ecological effect was that of changed competitive relationships in the recipient habitat (space monopolization or changed community composition, 98 case studies). These case studies consistently presented high abundances of the introduced species, with resultant space monopolization and reduced abundance or diversity of native macroalgae or associated fauna. A general decrease in abundance or richness of native macroalgal species in invaded areas compared with noninvaded areas was reported in 26 case studies. However, nine case studies (e.g., Schmidt and Scheibling 2006, Antoniadou and Chintiroglou 2007, Jones and Thornber 2010, Irigoyen et al. 2011a, Thomsen et al. 2013, Smith et al. 2014) reported an increase in the diversity (species richness) of epibionts (also as epifauna and epiphytes) or benthic macrofauna in NIMS-dominated habitats. More than 37 case studies (e.g., Chandrasekaran et al. 2008, Box et al. 2009, Janiak and Whitlatch 2012, Gribben et al. 2013), however, reported negative effects of introduced macroalgae on the reptile, fish, and invertebrate fauna in the recipient environment, with most cases reporting decreases in the number and abundance of species (Table 2).

Direct and indirect effects on other biota were associated with several species, including *Bonnemaisonia hamifera* (allelopathy deterring herbivory; Enge et al. 2012), *Caulerpa cylindracea* (phytotoxicity, bioaccumulation; Raniello et al. 2007, Terlizzi et al. 2011, Felline et al. 2014, Gorbi et al. 2014), *C. fragile* spp. *tomentosoides* (allelopathy deterring herbivory; Lyons et al. 2007), *Fucus evanescens* (Wikström et al. 2006, Forslund et al. 2010), *Lophocladia lallemandii* (epiphytized native brown algae had increased oxidative state; Tejada and Sureda 2014), and *Ceramium rubrum*/*Chaetomorpha linum* (associated sulfide production inhibiting sea grass growth; Holmer and Nielsen 2007). The presence of introduced *Hypnea musciformis*, *Acanthophora spicifera*, and *Gracilaria salicornia* was correlated with higher incidences of fibropapillomatosis, a debilitating tumor-forming disease in green sea turtles (Van Houtan et al. 2010). We found 16 cases of changes in habitat complexity, largely due to sediment accumulation after the establishment of introduced turf algae and 32 cases of effects on higher trophic levels (e.g., changes in the trophodynamism of amphipod assemblages, food web connectance, and community productivity). Two case studies reported a genetic effect (fertile hybrids between native and introduced congeners and selection for different phenotypes), thirteen case studies reported toxicity impacts (direct and indirect), and eleven case studies reported no significant impacts (although see discussion on the Challenges of Detecting Impacts section).

Table 3: Economic costs associated with eradication and control efforts for invasive macroalgae. Where no monetary value was available, an estimate of effort is given.

Species	Summary	Cost/effort	Location	References
Acanthophora spicifera	Summary of experiments with multiple methods (manual removal, shade, biological control) to reduce and/or remove from Kaloko Fishpond	Indirect: Manual removal would require 1–3 individuals working continuously to prevent recolonization of 4.5 ha pond	Kaloko Fishpond, Hawaii	Weijerman et al. 2008
Avrainvillea amadelpha	Removed from 9 ha of reef flats	Indirect: USD$20,994	Hawaii	Ken Longenecker, personal communication
Caulerpa cylindracea	Altered fatty acid composition in *Diplodus sardus*, a consumed fish, making it an improved source of essential fatty acids for human nutrition	No estimate provided	Mediterranean	Felline et al. 2014
Caulerpa taxifolia	Decreased yields for artisanal fisherman, increase in some costs (fuel, maintenance of gears and opportunity costs)	Direct: Not quantified	Tunisia	Salem and Gaamour 2007
Codium fragile	Mortality of cultured oysters; loss of ecosystem functions or values via displaced kelp	Direct: CAD$1,500,000 (characterized/year); CAD$11,994,000–$31,186,000 (projected/year)	Prince Edward Island, Canada	Coulatti et al. 2006
Codium fragile	High abundance within *Gracilaria chilensis* farms; negative impact on *G. chilensis* yield; costly handling and disposal of *C. fragile*	Direct and indirect: Upper limit to cost per unit effort at the 94th quartile	Chile	Neill et al. 2006
Neosiphonia harveyi	*N. harveryi* infects cultivated *Kappaphycus alvarezii*, resulting in significant reduction of commercial biomass production and decline in carrageenan quality	Direct: Infection rates of 7–69%	Philippines	Borlongan et al. 2011
Sargassum hystrix var. fluitans[a]	Clogged artisanal fishing gear and industrial trawl nets	Loss of work hours and reduced catch – no estimates provided	Nigeria	Solarin et al. 2014
Undaria pinnatifida	A collaborative effort led by Monterey Bay National Marine Sanctuary to monitor and remove *Undaria pinnatifida* from Monterey Harbor for a 10-year period.	Direct: US$160,300	Monterey Harbor, California, USA	Steve Lonhart, personal communication

[a] Species not found in Schaffelke and Hewitt (2007) review.

The majority of case studies focused on widely distributed and high-profile invaders: *C. cylindracea*, *C. taxifolia, C. fragile* ssp. *tomentosoides*, and *S. muticum*. These species exhibit high abundance and dominance in invaded systems. Since the original review (late 2005) and this update, both the recorded distribution and the number of impact case studies for each of these species have increased (Supplementary Table 1). We update the information about the nature and underlying mechanisms of ecological impact for the species presented in the following sections and also briefly discuss two case studies of introduced macroalgal assemblages: red algal introductions to the Hawaiian Islands and turf algae in the Mediterranean, whose cumulative effects have received recent attention.

Caulerpa cylindracea

Caulerpa cylindracea has been spreading in the Mediterranean Sea since the early 1990s (Verlaque et al. 2003, 2004, Klein and Verlaque 2008). In Italy, overgrowth by

C. cylindracea reduced diversity and abundance of native macroalgae, especially turf and encrusting species (Piazzi et al. 2001a). In mixed sea grass meadows of *Cymodocea nodosa* (Ucria) Ascherson and *Zostera noltii* Hornemann, *C. cylindracea* decreased shoot density of *C. nodosa* but increased density of *Z. noltii* (Ceccherelli and Campo 2002).

Where they co-occur, *C. cylindracea* is competitively superior to *C. taxifolia*, and growth rates of the former species are higher (Piazzi et al. 2001b, Piazzi and Ceccherelli 2002). The establishment of *C. cylindracea* most commonly led to the reduced abundance and species number of native algal growth forms: canopy-forming (Bulleri et al. 2010), as well as encrusting, foliose and articulated forms (Piazzi and Balata 2008, 2009). The decline in the latter three was attributed to increased sedimentation (Piazzi et al. 2007a). *Caulerpa cylindracea* was observed to reduce survival and biomass of live coral colonies (Kružić et al. 2008, Žuljević et al. 2011, Cebrian et al. 2012).

Several studies also demonstrated an impact on macroinvertebrates, such as lower amphipod richness and abundance, different species composition, and changes in food web structure compared with sea grass beds (Vázquez-Luis et al. 2008, 2009, Deudero et al. 2011, Lorenti et al. 2011, Pacciardi et al. 2011, Vázquiz-Luis 2013, Deudero et al. 2014). Finally, *C. cylindracea* was implicated in reducing the physical condition of white seabream (*Diplodus sargus* Linnaeus), via the bioaccumulation of the pest metabolite caulerpyne (Terlizzi et al. 2011).

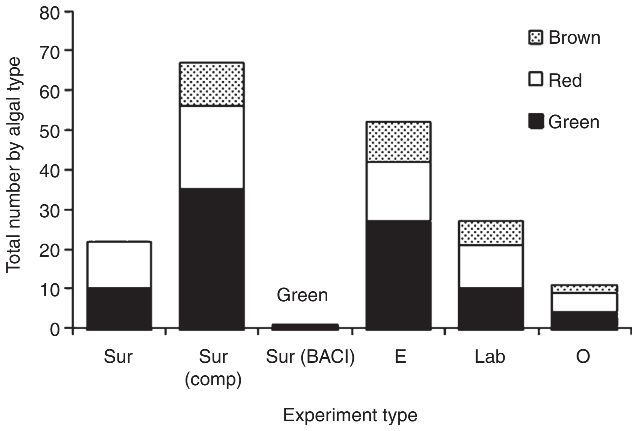

Figure 1: Ecological case studies by experiment type. Each study type divided by macroalgal group: brown algae (Phaeophyceae), red algae (Rhodophyta), green algae (Chlorophyta). Sur, field survey; Sur (comp), field survey comparing invaded and noninvaded sites; Sur (BACI), field survey with temporal comparisons before/after invasion; E, field experiment; Lab, laboratory experiment or assay; O, observational study.

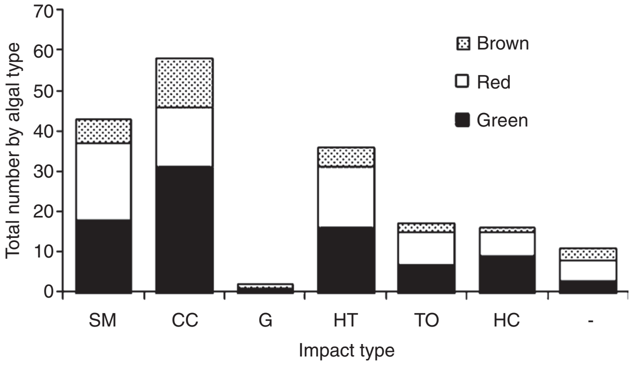

Figure 2: Ecological case studies by impact type. Each impact type divided by macroalgal group: brown algae (Phaeophyceae), red algae (Rhodophyta), green algae (Chlorophyta). SM, space monopolization; CC, change in community composition; G, genetic effects; HT, effects on higher trophic levels; TO, toxicity; HC, habitat change; (–), no significant impact shown.

The one potential human health effect found in the review was related to the potentially toxic effects of *C. cylindracea* on white seabream, which causes a change in the fatty acid composition of this fish (which is eaten by humans), making it an improved source of essential fatty acids for human nutrition (Felline et al. 2014). However, all impact studies were limited to the Mediterranean. Effects on diversity, total cover, and articulated algae persisted even after *C. cylindracea* had been removed. For example, Klein and Verlaque (2011) found lower values for these characteristics 18 months after *C. cylindracea* was removed. Although the invasion history of this species is relatively short, the research (e.g., Klein and Verlaque 2011) suggests that the current temporal reversibility of these impacts is likely to be moderate to high (recovery extending into decades or longer; Hewitt et al. 2011a, Ojaveer et al. 2015).

Caulerpa taxifolia

Research effort on the ecological impacts of *Caulerpa taxifolia* decreased relative to other invasive macroalgae, and the geographic focus shifted in large part from the Mediterranean Sea (1 study in this review) to Australia (12 studies in this review). However, this species continued to affect the diversity (Gallucci et al. 2012, Bishop and Kelaher 2013), growth, condition, and survival (Gribben et al. 2009) of invertebrates. Gribben et al. (2013) found that faunal impacts varied by community: *C. taxifolia* had a negative effect on infauna but a positive effect on epifauna. It also affected higher trophic levels by providing

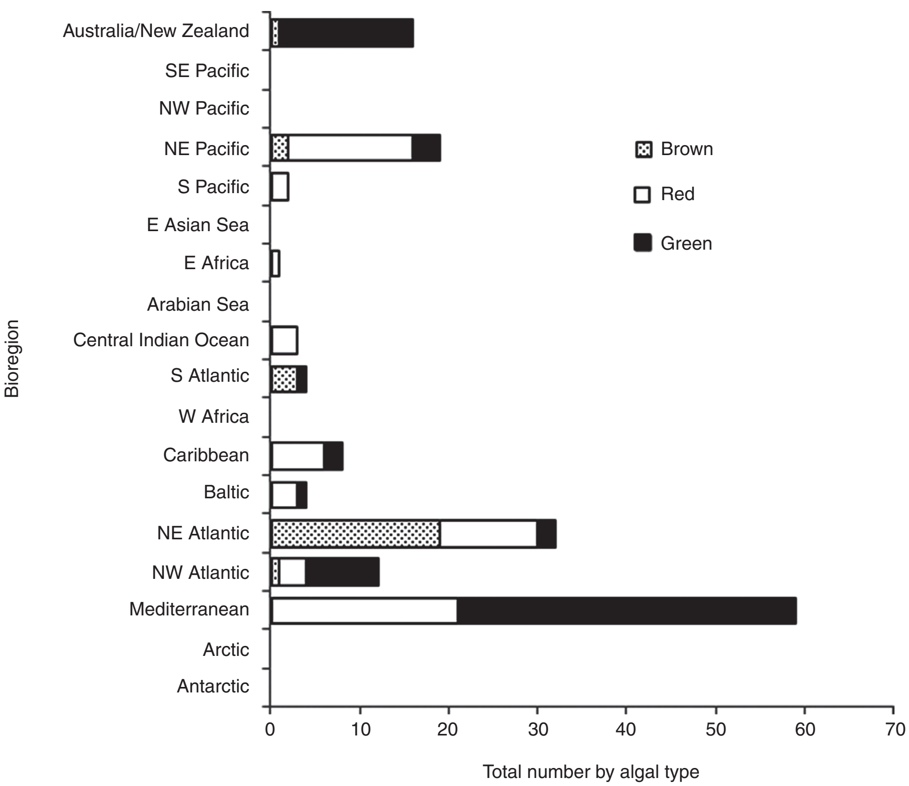

Figure 3: Ecological case studies by bioregion (bioregion classification based on Kelleher et al. 1995) and algal type. Macroalgal groups: brown algae (Phaeophyceae), red algae (Rhodophyta), and green algae (Chlorophyta).

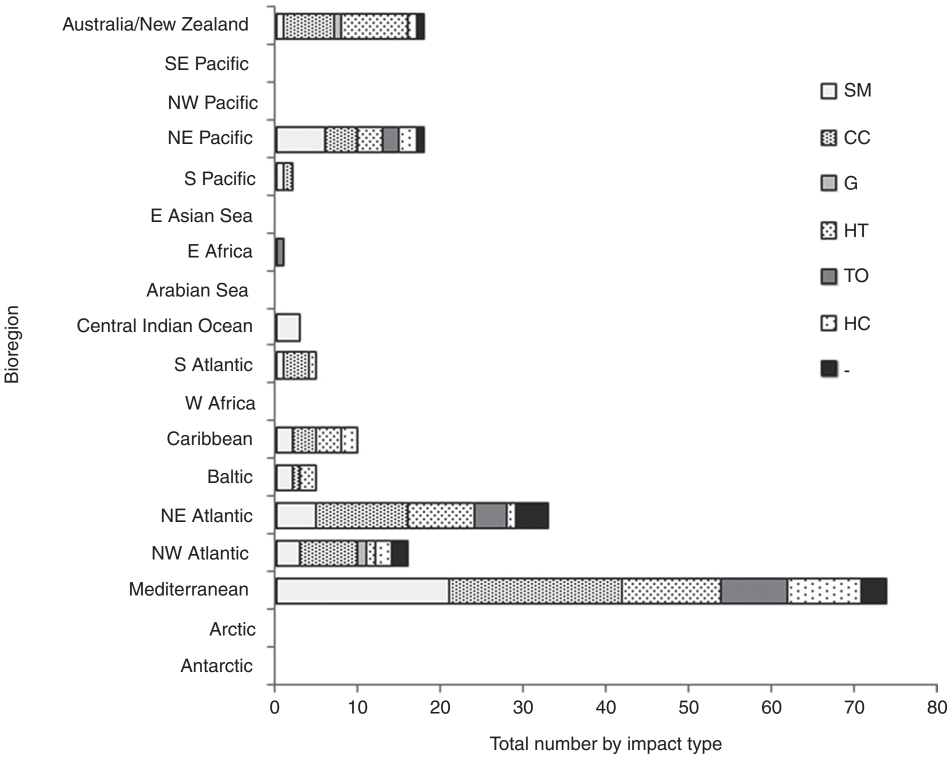

Figure 4: Ecological case studies by bioregion and impact type. Impact types: SM, space monopolization; CC, change in community composition; G, genetic effects; HT, effects on higher trophic levels; TO, toxicity; HC, habitat change; (–), no significant impact shown.

a less attractive food source to herbivores (Gollan and Wright 2006, Burfeind et al. 2009) and a less attractive fish habitat (York et al. 2006) relative to native macroalgae.

Codium fragile ssp. *tomentosoides*

Codium fragile ssp. *tomentosoides* maintained its dominance in many areas of the northwest Atlantic because it is a superior competitor after disturbance events (Scheibling and Gagnon 2006, Kelly et al. 2011). However, several studies reported greater macrofaunal and epiphyte diversity associated with *C. fragile* ssp. *tomentosoides* (Schmidt and Scheibling 2006, 2007), which may be due to increased adaptation of the local community to this species (Harris and Jones 2005). A single study outside the northwest Atlantic showed that *C. fragile* ssp. *tomentosoides* increased the recruitment of the mussel *Mytilus galloprovincialis* Lamarck (Bulleri et al. 2006).

Sargassum muticum

Several of the case studies of the impacts of *Sargassum muticum* introductions showed negative effects, such as being an undesirable food source for herbivores (Monteiro et al. 2009), suppression of native algal assemblages (Olabarria et al. 2009), and space monopolization (Thomsen et al. 2006). However, several of the studies had ambiguous results, with some taxonomic groups showing increased abundance and some showing decreased abundance (Lang and Buschbaum 2010, Gestoso et al. 2012). *Sargassum muticum* also enhanced epibiotic diversity in soft-bottom environments (Buschbaum et al. 2006), and at time scales of <1 week after colonization (Rodil et al. 2008). This species was a preferred forage material for the snail *Lacuna vincta* Montagu (Britton-Simmons et al. 2011), and its presence increased overall faunal abundance (Strong et al. 2006).

Impact of introduced macroalgal assemblages

In the 2007 review, several red algal species (*A. spicifera*, *Avrainvillea amadelpha*, *G. salicornia*, *H. musciformis*, *Kappaphycus* spp., and *Eucheuma* spp.) were reported to have established at high abundances and to have spread on Hawaiian coral reefs (Smith et al. 2002, Conklin and Smith 2005, Weijerman et al. 2008). Several factors are implicated in these invasions, including low herbivory on introduced species (Vermeij et al. 2009) and increased nutrient pollution due to urbanization (e.g., stormwater outflows; Lapointe and Bedford 2011). These red algal species increase overall macroalgal productivity and biomass on coral reefs and reduce invertebrate diversity (Longenecker et al. 2011) or shift community dominance (e.g., increased detritivore diversity; Fukunaga et al. 2014). *Gracilaria salicornia* reduces irradiance, increases sedimentation, and changes diurnal dissolved oxygen and pH cycles, potentially affecting the habitat quality for corals (Martinez et al. 2009, 2012). Mats of *C. rubrum* and *C. linum* reduce oxygen in the water column and increase sulfide levels in the sediment, resulting in the degradation of the sea grass *Zostera marina* L. (Holmer and Nielsen 2007).

Several studies examined mats with multiple introduced macroalgal species and found similar impacts. Interestingly, the relative importance of *C. taxifolia* and *C. cylindracea* varied in mats where they both occurred. Holmer et al. (2009) found limited effects from *C. taxifolia* compared with *C. cylindracea*, whereas Montefalcone et al. (2007a) found that the substitution of *Posidonia oceanica* (L.) Delile by *C. taxifolia* was greater than that by *C. cylindracea*. The latter observation, however, is likely to have been influenced by the longer duration of the *C. taxifolia* invasion. In addition to effects on macroalgae, the co-occurrence of *Womersleyella setacea* and *Acrothamnion preissii* led to a fivefold reduction in recruitment and reduced biomass and a threefold increase in juvenile mortality of gorgonian coral *Eunicella singularis* (Esper, 1791) (Linares et al. 2012).

Economic impacts

Published information about economic and societal impacts of introduced macroalgae was scarce (Table 3). Many reports consisted of control or eradication costs for species-specific management. Although there was some anecdotal information on governmental management, research, and education/extension costs, the information was too limited to draw any general conclusions. The best estimates came from indirect costs associated with response and control efforts (Table 3). In one instance, we identified detailed costs of removal efforts: Longenecker (personal communication) for *Avrainvillea amadelpha* in Hawaii (Table 3).

Amenity and recreational value impacts of introduced macroalgae can be expected at high abundances, or where aspect dominance is achieved. However, estimates of revenue loss caused by incursions of introduced macroalgae were not available and were limited to descriptions of potential losses. For example, *U. pinnatifida* may threaten UNESCO ecotourism sites that depend on high biodiversity and aesthetic quality (Irigoyen et al. 2011b), and decomposing *H. musciformis* may reduce tourism via fouled beaches (Huisman et al. 2007).

We were also unable to find any quantitative information about societal impacts or ramifications of macroalgal introductions, such as the effect of reduced availability of the native algal species in Hawaii (limu), which are important as food and medicine, and for ceremonial use (Abbott 1984, McDermid and Stuercke 2003).

Discussion

Factors influencing the ecological impacts of introduced macroalgae

The 60 studies included in the previous review of the impacts of introduced macroalgae (Schaffelke and Hewitt 2007) spanned two decades of research. The additional 142 studies available a decade later demonstrate an increase in attention to this group of invaders. Although the number of species studied for potential impacts increased from 17 to 30 (species not included in Schaffelke and Hewitt 2007 are indicated by ([a]) in Tables 2 and 3), this still represents only a small fraction (~10%) of the current estimated total number of globally introduced macroalgal species (circa 315; Hewitt et al. unpublished data). This low representation of this type of research in the literature agrees with the review by Williams and Smith (2007), which found that environmental impact data were available for only 6% of introduced algal species.

Spatial coverage also continues to be biased: 7 of the 18 bioregions had no information on the impacts of introduced macroalgae. The Mediterranean remained the “hot spot” for research, with about a third of the studies. Thus, despite progress, there remains an urgent need for more information to guide NIMS management (e.g., Parker et al. 1999, Ruiz et al. 1999, Gurevitch and Padilla 2004, Hewitt et al. 2011a, Ojaveer et al. 2015). This research should expand to include a greater taxonomic and spatial scope, in particular. Within the social sciences (as discussed below), this research needs to expand to include studies on economic and societal impacts and implications.

There were several notable trends demonstrated in the reviewed literature. First, only one study employed a before-after control-impact (BACI) design, whereas surveys comparing invaded and uninvaded habitat were the most common study type (Figure 1). This scarcity of BACI designs has been another weakness in invasion biology research, as this method has the highest potential to demonstrate impact (e.g., Byers et al. 2002, Kumschick et al. 2015). Second, as mentioned previously, research continues to be limited to a small proportion of biogeographic regions (Figures 3 and 4). Third, the most common impact types were changes in community composition and space monopolization (Figure 2). These impacts do not occur in isolation, however, and are a function of both the invader and the invaded environment (Dunstan and Johnson 2007, Schaffelke and Hewitt 2007, Valentine et al. 2007), which is further discussed below.

Influence of the recipient environment

The influence of the recipient environment on invasion success has received significant attention and formed the basis of species distribution models in anticipating establishment and ultimate spread (Elith and Leathwick 2009). By contrast, the influence of the recipient environment, and more importantly the receiving community, on the level and degree of ultimate impact has not been explored in detail.

Disturbance has been identified as a factor that may facilitate initial establishment, persistence, and subsequent spread of NIMS (Davis et al. 2000, Mack et al. 2000, MacDougall and Turkington 2005, Britton-Simmons and Abbott 2008, Dunstan and Johnson 2007, Valentine et al. 2007). Natural disturbances, such as storm surges, can alter the physical habitat. Scheibling and Gagnon (2006) created gaps that mimicked those generated by disturbance, whereby *C. fragile* ssp. *tomentosoides* not only out-competed native macroalgae in these gaps but also continued to exclude recolonization by native taxa.

Anthropogenic disturbances, such as increased nutrient or sediment inputs from agricultural and urban areas and aquaculture facilities, can alter the environmental conditions to the benefit of invasive macroalgae. Lapointe and Bedford (2011) demonstrated that nitrogen from stormwater inputs yielded a competitive advantage to *A. spicifera*. With increased proximity to a stormwater outfall in Hawaii, invasive algal abundance increased whereas native algae decreased. Gennaro and Piazzi (2011, 2014) revealed that nutrient enrichment enhanced the spread of *C. cylindracea* and amplified its negative effects on native macroalgal abundance. Montefalcone et al. (2007b) demonstrated that these phase shifts are often permanent. Where *C. nodosa* and *C. cylindracea* replaced *P. oceanica* near urban centers, recolonization by the endemic sea grass was considered unlikely due to the very slow growth rates of *P. oceanica* (Montefalcone et al. 2007b).

It is worth noting that anthropogenic disturbances are likely to enhance nuisance blooms of native macroalgal species in many regions (e.g., Wang et al. 2009, Hu et al. 2010). These outbreaks can cause significant impacts (e.g., more than US$100 million in control costs for *Ulva prolifera*; Hu et al. 2010). Although these native "pests" are not a focus in the current context, they represent a parallel source of information for the understanding and management of outbreaks in general.

Williams and Smith (2007) identified that the effects of the recipient environment differ between functional groups. Filamentous species (e.g., *Acanthophora*, *Polysiphonia*, and *Womersleyella*) appear more likely to flourish in areas with high physical disturbance, such as ports and harbors. Foliose macroalgae (e.g., *Ulva*) seem to succeed in areas with moderate physical disturbance and nutrient availability. Large leathery macroalgae (e.g., *Undaria*, *Sargassum*, and *Fucus*) are expected to do best in areas with high nutrient availability (Williams and Smith 2007; B. Schaffelke, personal observation).

Removal of native macroalgal communities can result in the increased recruitment of *S. muticum* (Britton-Simmons 2006), whereas increased native diversity can lead to lower *S. muticum* abundance (field survey) and reduced growth and survival (experimental study; White and Shurin 2007). Similarly, *C. cylindracea* and *C. taxifolia* showed increased colonization of degraded areas, such as dead sea grass mattes, compared with live meadows (Bulleri et al. 2011, Infantes et al. 2011). This evidence of differential recruitment and colonization of NIMS should provide an additional incentive to protect threatened habitat or restore areas that have been degraded to prevent incursion, establishment, and spread of NIMS.

Finally, release from natural predators (herbivores) may be another important mechanism that enhances impact. Through feeding preference, grazers may further reduce the abundance of already diminished native species relative to introduced NIMS, thus exacerbating the degree of impact (Kotta et al. 2004, Gollan and Wright 2006, Wikström et al. 2006, Lyons et al. 2007, Weinberger et al. 2008, Monteiro et al. 2009, Forslund et al. 2010, Tomas et al. 2011, Enge et al. 2012). However, Vermeij et al. (2009) found greater herbivory on NIMS relative to Hawaiian native macroalgae, and Harris and Jones (2005) found herbivory by the sea slug *Placida dendritica* (Alder and Hancock 1843) was greater on older *C. fragile* spp. *tomentosoides* stands.

Influence of species' functional traits

Analyses of species' traits that predict impacts have occurred in both freshwater and marine contexts (Nyberg and Wallentinus 2005, Schultz and Dibble 2012). Traits associated with negative impacts included comparably higher growth rate, allelopathic chemical production, and phenotypic plasticity. These characteristics facilitated improved competitiveness within the same environmental conditions relative to native species. However, other studies have found that rapid colonization and spread of introduced macroalgae (analogous to growth rates in the freshwater review) were not correlated with negative impacts on biodiversity (Ricciardi and Cohen 2007). Impacts are also likely to be scale dependent, such as varying with the overall size of the invaded area and/or the abundance of the invasive macroalgae (Drouin et al. 2012).

Confounding the influence of traits is the observation that conspecifics or congenerics often have similar traits but demonstrate no adverse impact (Paula and Eston 1987, Trowbridge 1996, Vroom and Smith 2001, Nyberg and Wallentinus 2005). In this review, we noted impact studies for three additional congeners of the "infamous" *C. taxifolia*. It is unknown whether this is a result of more attention to this well-known genus or traits specific to *Caulerpa* species.

Climate change

Biological invasions and climate change have been acknowledged independently as severe threats to ecological integrity worldwide. Yet inquiry and analysis of the interactions between climate change and invasions is a nascent field despite repeated calls for research (Occhipinti-Ambrogi 2007, Moore et al. 2008, Williams and Grosholz 2008). Occhipinti-Ambrogi (2007) discusses the potential effects of climate change on marine invasions, including dispersal mechanisms and competitive interactions between invaders and natives. Direct effects may include those on individual physiology and dispersal, leading to changes in population dynamics and community structure. Indirect effects include changes in species distribution, diversity, productivity, and microevolution (Harley et al. 2006, Occhipinti-Ambrogi 2007).

Few studies have looked at the effect of climate change on the competition between native and introduced marine taxa (but see Sorte et al. 2010a,b, Zerebecki and Sorte 2011, which found that introduced species tolerate higher temperatures better than native species). Higher growth and reproductive output were observed with increased temperatures, in both shallow and deep populations of the introduced red alga *L. lallemandii* (Cebrian and Ballesteros 2010). Martinez-Luscher and Holmer (2010) found that the negative effects of *Gracilaria vermiculophylla* on *Zostera marina* (reduced metabolism and survival) increased with temperature.

Challenges in detecting impacts

The challenge of accurately assessing NIMS impacts is twofold. The first challenge is undertaking impact studies for the range of taxa that exist and over the large geographic ranges where they exist. Identifying established NIMS is difficult because of insufficient taxonomic expertise and baseline data to determine which species are native and which have been introduced (e.g., Ruiz et al. 1999, 2000, Campbell et al. 2007). Achieving a balanced understanding of invasions across spatial and temporal scales is also difficult. Studies continue to primarily occur, and thus find NIMS, in invasion "hot spots" (Ruiz et al. 2000, Hewitt and Martin 2001, Ruiz and Hewitt 2002, Hewitt 2003, Campbell et al. 2007). These areas are often urbanized and have a high propagule pressure of potentially invasive species (Ruiz and Hewitt 2002, Hewitt et al. 2004b, Hewitt et al. 2011a). Although increased monitoring efforts yield valuable distribution data, they generally do not deliver information about impacts of introduced species (e.g., Meinesz 2007).

The second challenge is the assumption that impacts are correctly identified. This challenge has two distinct elements: our ability to ascertain impacts and our ability to scale (i.e., quantify or categorize) impacts. Given that most risk assessments for NIMS advocate using available science-based knowledge (e.g., Dahlstrom et al. 2010, Campbell and Hewitt 2011), these two elements are of critical importance to enable individual species to be considered as a threat (e.g., Hewitt et al. 2009a).

Ability to ascertain impact

Our ability to identify impacts of individual species is typically analyzed via null hypothesis significance testing (NHST; Nakagawa and Cuthill 2007). NHST uses statistical analyses to determine whether one rejects, or fails to reject, a null hypothesis of "no effect", based on the probability (p-value) that the findings are unlikely to be within the population of the control (generally set at 0.05; Lehmann and Romano 2005). Although a useful tool, criticism of NHST has focused on several areas, including its effect on statistical power. The power (of a test) is the probability of correctly rejecting the null hypothesis and the complement of the type II error rate β, 1-β (Lehmann and Romano 2005, Nakagawa and Cuthill 2007). Power is a function of the following interdependent components (Equation 1): sample size (n), significance criterion (α and β), effect size (ES), and σ (population standard deviation) (di Stefano 2003, Nakagawa and Cuthill 2007); that is,

$$\text{Power}=(1\text{-}\beta)\propto(\text{ES}\times\alpha\times\sqrt{\text{n}})/\sigma \tag{1}$$

The focus on a low acceptable type I error (α=0.05) that occurs in NHST (exemplified by the publications in this review) can thus lead to low power and high rates of type II errors. Lower power is exacerbated by inadequate experimental design, such as small effect and sample sizes, which is common in NIMS studies. This low power can lead to misinterpretation of a "nonsignificant" finding as "no impact" (Davidson and Hewitt 2014). Power is rarely determined or reported in publications (Rosnow and Rosenthal 1989), despite the implications of low power and type II errors in invasive species management (e.g., masking real effects on a native species, community or ecosystem). Davidson and Hewitt (2014) found only 3% of NIMS studies had sufficient power (using recommended minimum criterion of 0.8 power; Cohen 1977), despite relatively large effect sizes.

The potential for "missing" impacts and high rates of type II errors seems a likely, or at least unexamined, phenomenon within the publications of this review. Several of the articles reported nonsignificant results but did not report power. For example, Rohr et al. (2011) reported no difference in the recruitment of the snail *L. vincta* based on epiphyte composition (p=0.14), despite large variation, small effect sizes, and a relatively small sample size (n=10). In Piazzi and Ceccherelli (2006), the cover of each vegetation layer did not vary "significantly" between *C. cylindracea* cleared and invaded plots, but neither power nor p values are provided despite low sample sizes (n=2). The same limited reporting of statistical details is seen in Longenecker et al. (2011) (n=8), Davis et al. (2005) (n=7–29, most around 10), Olabarria et al. (2009) (n=5), and Bulleri et al. (2010) (n=5). Although identified to prove a point, these studies are certainly not the exception to the rule but rather the rule: none of the publications reviewed herein reported statistical power, and only two discussed the potential for few replicates and high variation to lead to low power (Lorenti et al. 2011, Drouin et al. 2012). Hence, although most of the analyses found significant impacts, those "nonsignificant" analyses should be interpreted with caution. Some invasive macroalgae may indeed have no impact for a specific interaction, but power estimates should accompany these conclusions.

Ability to scale impacts

The second element of correctly identifying impacts of NIMS stems from our ability to rank the level of impact on an ordinal or categorical scale. Several researchers have attempted to develop impact or consequence exemplars to provide a basis to evaluate across species and ecosystems (e.g., Campbell 2006, 2008, 2011, Hewitt et al. 2009a, 2010, Kumschick et al. 2012, Campbell and Hewitt 2013, Blackburn et al. 2014). For example, Campbell (2006, 2008, 2011) and Hewitt et al. (2006, 2011a) have provided a suite of "consequence matrices" that provide examples of impact to multiple values (e.g., environmental, economic, social, and cultural) as an input to a risk assessment process that incorporates both qualitative and quantitiave data. By contrast, Blackburn et al. (2014) have recently proposed an impact framework (a structure that assists in classifying the type and size of an impact) that provides examples across different mechanisms of impact (e.g., competition, predation, and parasitism). This latter framework aligns with the categories we use in this review and is appropriate to aid in invasion research but provides limited utility for managers (see discussion in Ojaveer et al. 2015).

Unfortunately, there are not enough data to categorize impacts for the majority of marine species and value sets (Hewitt et al. 2009a). This suggests that recent calls to shift biosecurity frameworks away from managing introductions toward managing impacts (e.g., Davis et al. 2011, Blackburn et al. 2014, Kumschick et al. 2015) will result in a greater exposure to unknown and unrecognized risks.

Economic and societal impacts

The scarcity of research on the economic impacts of introduced macroalgae precludes any summary or general assessment of trends. This knowledge gap was identified in the previous review (Schaffelke and Hewitt 2007) and appears not to have been addressed in the literature since (Freshwater et al. 2006, Schaffelke et al. 2006, Williams and Smith 2007, Williams and Grosholz 2008, but see Colautti et al. 2006, Neill et al. 2006), despite a large research effort on identifying and valuing ecosystems (including marine) and their services (e.g., Troell et al. 2006, Worm et al. 2006, Beaumont et al. 2007, Samonte-Tan et al. 2007, Daily et al. 2009, Fisher et al. 2009, Lange and Jiddawi 2009, Mace et al. 2012). The direct impacts that have been observed generally stem from economic losses in aquaculture or fisheries.

Within the temporal frame of our review (2005–2014), we found only one study that directly addressed social, cultural, or human health impacts from introduced marine macroalgae (Felline et al. 2014). Despite the paucity of research in these areas captured by this review, we are aware that some evaluations of socioeconomic impact have occurred (e.g., Samonte-Tan et al. 2007, Campbell and Hewitt 2013). We discuss below some socioeconomic valuation papers that consider introduced macroalgae but failed to recognize or attribute these species as NIMS in their assessments, e.g., of the economic value of seaweed aquaculture (e.g., Samonte-Tan et al. 2007).

Ecosystem service valuations report both negative and positive economic impacts of introduced macroalgae. For example, Pickering et al. (2007) argue that intentionally introducing macroalgae [such as *U. pinnatifida* and *Kappaphycus alvarezii* (Doty) Doty *ex* P.C. Silva] provides benefits that outweigh many perceived costs. The socioeconomic benefits of macroalgal farming are export earnings, diversified aquaculture production, and local employment opportunities, especially in developing countries (Troell et al. 2006, Samonte-Tan et al. 2007, Neori 2008, Lange and Jiddawi 2009), as well as producing high value compounds for chemical and biotechnology industries (e.g., Rönnbäck et al. 2007, Morrissey et al. 2011). However, ecosystem service valuations often fail to fully consider the trade-offs of farming NIMS (e.g., Troell et al. 2006, Samonte-Tan et al. 2007, Lange and Jiddawai 2009). For example, farming of *K. alvarezii* continues to expand despite information that indicates negative ecological impacts of this species in its introduced range (e.g., Sulu et al. 2003, Chandrasekaran et al. 2008, Kamalakannan et al. 2010, 2014), which may have widespread negative follow-on effects to other marine-based industries such as tourism and harvest fisheries.

Samonte-Tan et al. (2007) provide estimates of income-generated benefits for farming macroalgae (*K. alvarezii* and *Eucheuma* sp.) of US$52–96 per month for farmers in the Philippines. Yet the income generated from other marine industries in the Philippines far outweighs that generated by seaweed farming (e.g., monthly estimates: US$307 boat tourism, US$2,090–2,907 coastal hotels and resorts, and US$2,998 dive shops). In Ireland, the estimated gross value added (GVA) from native algae and biotechnology is €14,552,000, and marine services such as shipping and maritime transport and marine tourism generate a GVA of €1,343,579,000 (Morrissey et al. 2011). All of these marine and coastal industries have the potential to be directly and indirectly affected by macroalgal invasions (e.g., Hewitt et al. 2006, Campbell and Hewitt 2013).

Although analyses of ecosystem services can be useful to resource management (Mace et al. 2012), we propose that, until it is clearly established that the economic benefits outweigh the long-term ecological and socioeconomic impacts of intentional introductions, preference should be given to the culture of native macroalgae, and that robust strategies to prevent and control macroalgal introductions should remain essential (Andreakis and Schaffelke 2012). Finally, future evaluations should consider ecological and social as well as economic impacts (e.g., Campbell 2006, Campbell and Hewitt 2013).

Research needs

In 2007, Schaffelke and Hewitt identified the need for multidisciplinary research with biological, social, and economic approaches to the impacts of introduced macroalgae. Specifically, they called for a greater understanding of the human-driven transport and establishment mechanisms that precede the impact stage. At present, there is more information on the behavioral intent and perceptions of risk associated with the introductions (intentional and unintentional) of species (e.g., Azmi 2010, Cliff and Campbell 2012, Davidson et al. 2013, Trenouth and Campbell 2013), which can be used to improve management and education. However, studies that examine the social and community implications of introduced macroalgae remain as major research gaps (but see Campbell 2006). This knowledge gap is critical, as the management of introduced species is often transferred to the public domain (e.g., Crowl et al. 2008, Delaney et al. 2008, Bryant 2011). To effectively engage, the public requires an incentive that clearly demonstrates the impacts and benefits of NIMS within peoples' social and economic context (Trenouth and Campbell 2013). Impeding additional research in all impact areas is the effect of the global financial crisis, which has resulted in dwindling funds for managing invasions (e.g., Lucy and Panov 2014, MacNeil and Campbell 2014).

In general, economic assessments related to marine-introduced species have focused on harmful algal blooms (microalgae; e.g., Van den Bergh et al. 2002, Pimentel 2005) and fish species (e.g., Gozlan and Newton 2009, Gozlan 2010), with very few studies focusing on the economic costs of macroalgal invasions. Boudouresque (2002) briefly touched on the possible economic impacts of introduced macroalgal species within the Mediterranean. He identified a research gap when he postulated that the economic benefits of an introduced species go beyond direct costs (related to sales prices); comprehensive cost-benefit analyses that take into account collateral damage and externalized costs across a broad market (and nonmarket) are required for a full understanding.

Also identified by Schaffelke and Hewitt (2007) is the need for frameworks that better predict which species are likely to invade which habitats. Progress has been made in this area (e.g., Hayes et al. 2004, Inglis et al. 2006, Hewitt et al. 2011b). Climate change remains on the research agenda, as does the spatial and temporal variability of impacts. This is particularly true in areas where climate change may be most severe and in areas that are underrepresented in impact research, such as coastal zones of developing countries and island states. This knowledge will support efforts to address Article 8h of the Convention of Biological Diversity (prevention, control, and eradication of introduced species that threaten ecosystems or species) and subsequent obligations to fulfill this mandate, as directed in Decisions by the Conference of the Parties (CBD Secretariat 1992). This research should also consider the application of precaution in managing NIMS amid a changing economic and environmental climate, as also mandated by the Convention of Biological Diversity.

Conclusions

Although impacts are the last stage in the invasion process (following introduction, establishment, and spread), preventing these impacts often motivates NIMS management at an earlier stage. Most management efforts focus on preventing the introductions, given this "choke point" has the highest probability of avoiding impact (e.g., Hewitt 2003, Hewitt et al. 2004a, 2011a). As prevention activities are never completely effective, however, early detection efforts that target NIMS at the establishment or early spread stage are recognized as an essential element of the biosecurity toolkit (Vander Zanden and Olden 2008). Finally, the management of impacts can occur by limiting NIMS abundances through active control measures, for example, see Anderson (2007) and Wotton and Hewitt (2004).

Although this review found a large increase in published research on the impacts of macroalgal invasions, the information remains too sparse to identify general patterns that allow a prediction of which species are likely to have significant negative impacts, or where such impacts would occur. For example, the impacts of the relatively recent introduction of *C. cylindracea* into the Mediterranean are now regarded as more serious than those of *C. taxifolia* (Klein and Verlaque 2008). Subsequently, research effort has shifted away from *C. taxifolia* (see Table 2). Research into the socioeconomic impacts of introduced macroalgae remain scarce and are largely limited to anecdotal accounts. This represents a major failing and hindrance to the effective management of introduced macroalgae. Such management depends on published literature to develop, implement, and refine cost-effective solutions for early detection and rapid response efforts. With accelerating rates of climate and other global change, the poorly understood patterns in invader distribution and impacts are likely to change, and more substantial effort needs to be made to improve predictions of biological invasions.

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