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Review

Impacts of introduced seaweeds

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Abstract

We analyzed 69 publications on the impacts of introduced seaweeds. The predominant impacts were changed competitive relationships in the recipient habitat, indicated by high abundances of invaders, resultant space monopolization, and reduced abundances/biomass of native macrophytes. Changes in biodiversity, effects on fish and invertebrate fauna, toxic effects on other biota, and habitat change were also identified. The mechanisms underlying the manifestation of impacts are uncertain and inferences about common patterns were hampered because impact studies were available for only a few introduced seaweeds, covered only a fraction of their introduced distribution and generally were conducted over short time scales. There was no information about evolutionary effects or changes of ecosystem processes. Knowledge of socio-economic impacts of invasive seaweeds is poor. We collated costs associated with control/eradication activities and for national spending on marine biosecurity in Australia, New Zealand and the United States. Prevention of impacts is the driving force for costly surveillance, eradication and control programs. Until we are able to understand, predict and measure impacts of introduced seaweeds, the management of species incursions needs to remain focused on early detection, rapid response and control to reduce the likelihood of negative impact effects.

Keywords: control; ecological impacts; economic impacts; eradication; introduced macroalgae.

Introduction

It is now widely accepted that global marine biodiversity and resource values of the world's oceans are threatened by anthropogenic influences. In particular, overfishing, habitat alteration and destruction, global climate change and the introduction of alien marine species are identified stressors, especially in coastal regions (Norse 1993, Vitousek et al. 1997, Carlton 2000). The rate of marine introductions, including introductions of seaweeds, has

increased over the last 20 years, reflecting increased global trade and changes in economic activities; however, more awareness of the problem and increased survey effort are likely to have increased the detection of introductions (Ruiz et al. 2000, Perrings et al. 2002, Ribera Siguan 2002, Hewitt 2003a; see also Costello and Solow 2003).

The assessment of ecological impacts of alien marine species has been recognized as a research priority in recent years. However, there are still very few rigorous studies of the impacts of aliens (Ruiz et al. 1999, Grosholz et al. 2000, Grosholz 2002). The threats posed are often inferred from estimates of introduction status and observations of negative impacts in other invaded areas, especially when aliens attain high abundances in a particular ecosystem. An alternative view is that most marine alien species have negligible impacts on their recipient environment, or are merely an addition to the ecosystem (Farnham 1980, Reise et al. 1999). However, there are some well-known examples of catastrophic effects of marine alien invaders on recipient ecosystems, e.g., the Asian clam [*Potamocorbula amurensis* (Schrenck)] in San Francisco Bay (Nichols et al. 1994), the comb jelly [*Mnemiopsis leidyi* (A. Agassiz)] in the Black Sea (Kideys 2002), and the predatory sea star *Asterias amurensis* (Lütken) in Tasmania and Victoria, Australia (Ross et al. 2003). Evidence is now also mounting that synergistic effects with other stressors play an important role for the establishment and spread of marine alien species, and, hence, for any negative impacts (Ruiz et al. 1999, Occhipinti-Ambrogi and Savini 2003). Ecosystem alterations due to global change coupled with species introductions are thought to result in "biotic homogenization" (e.g., Olden et al. 2004, Olden and Poff 2004, Wilkinson 2004), a process by which ecosystems will become dominated by generalists and opportunistic species. This pattern has already been observed in some locations affected by environmental degradation and species' invasions (McKinney and Lockwood 1999). Formal assessment frameworks for impacts of marine aliens, or introduced species in general, are scarce, both for ecological effects and for associated economic costs (Parker et al. 1999, Ruiz et al. 1999, Pimentel et al. 2000, Perrings et al. 2002, Hewitt 2003b).

Marine macroalgae (seaweeds) are a significant component of marine alien taxa (Schaffelke et al. 2006) with current global estimates of introduced macroalgae ranging from 163 (Ribera Siguan 2002) to 260 species (J.E. Smith unpublished data). The current knowledge of impacts of alien macroalgae is even sparser than for other taxonomic groups of aliens. This is in contrast to the perception that invading macroalgae have potentially serious impacts, because they may alter ecosystem structure and function by monopolizing space, develop-

ing into ecosystem engineers, and altering foodwebs. Of particular concern is their potentially rapid spread beyond initial points of introduction through efficient dispersal, coupled with significant environmental and economic consequences (Thresher 2000). Documented impacts of seaweed invaders are known mostly from a few, well-studied, high profile species [e.g., *Caulerpa taxifolia* (Vahl) C. Agardh, *Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (Van Goor) Silva, *Sargassum muticum* (Yendo) Fensholt and *Undaria pinnatifida* (Harvey) Suringar; e.g., Ribera and Boudouresque 1995, Trowbridge 1998, Walker and Kendrick 1998, Boudouresque and Verlaque 2002, Levin et al. 2002, Ribera Siguan 2002, Wallentinus 2002, Occhipinti-Ambrogi and Savini 2003, Schaffelke et al. 2006].

In this review we synthesize and analyze current knowledge of impacts of alien seaweeds using published sources. We categorize reported impacts and classify the quality of the information (e.g., observational information, data from manipulative field experiments). Our aim is to find patterns of impacts, to examine whether certain species are more likely to cause significant impacts than others, and to identify mechanisms contributing to the observed impacts.

Methods

We examined 69 publications (~1980s to 2005) that present data on impacts of alien seaweeds; reviews and publications offering only distributional or observational data were omitted. Some original publications cited elsewhere proved difficult to obtain (e.g., reports to government agencies, unpublished proceedings). These are cited as the original author(s) based on the secondary source (e.g., Wear and Gardner 1999, cited in Sinner et al. 2000). Studies that reported results from several alien species were listed as separate case studies for each species, unless they explicitly addressed interactions between the species. Results reported in multiple publications but leading to the same conclusion with regard to impact were listed as one case study, with all relevant references.

Impacts or risks of impacts have been variously categorized (e.g., Gollasch and Leppäkoski 1999, Parker et al. 1999, Ruiz et al. 1999, Grosholz 2002, Hewitt 2003b). For the purpose of this review we consider potential impacts into the following categories:

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, 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/non government)
 - Costs of research into introduced species
 - Costs for eradication and control measures
 - Costs for education/extension campaigns.

Information about economic impacts was collated from quantitative assessments of cost or effort for control and eradication measures. While there are potentially other kinds of economic impacts (see list above), this was the only type of socio-economic impact for which there were sufficient quantitative data.

Ecological impacts

The 60 collated case studies report ecological impacts for only 17 species of introduced seaweeds (Table 1). These existing studies of impact address only a small fraction (~6.5%) of the current estimate of the total number of globally introduced macroalgal species (circa 260).

The predominant effect of alien macroalgae reported in the case studies were changed competitive relationships in the recipient habitat (43 case studies, Table 1). These were generally indicated by high abundances of the alien species, resultant space monopolization and reduced abundances/biomass of native macroalgae or seagrasses. Changes in biodiversity, generally a decrease in richness of native macroalgal species in invaded areas compared to non-invaded areas, were reported in nine case studies. An additional 13 case studies reported effects of alien macroalgae on fish and invertebrate fauna in the recipient environment, with most cases reporting decreases in the number and abundance of species (Table 1). Six examples of toxic effects on other biota were reported for *Caulerpa* species. Less clear is the occurrence of habitat change, such as changes in productivity or habitat complexity (e.g., addition or loss of canopy species); seven case studies report such changes, mainly, however, based on observations or assumptions. One case study reported a genetic effect, the occurrence of fertile hybrids between an alien and a native congener (Table 1). Three case studies found no significant impacts of the alien seaweed studied. We were unable to find quantitative information about evolutionary effects or about changes in ecosystem processes caused by seaweed introductions.

The majority of case studies focused on *Caulerpa taxifolia*, followed by *Undaria pinnatifida*, *Sargassum muticum* and *Codium fragile* ssp. *tomentosoides*. These species are the geographically most widely distributed alien macroalgae, and they are also able to attain high

Table 1 Summary information of case studies of impacts of alien macroalgae.

Species		Summary	Method	Effect	Location	Reference
<i>Acanthophora</i> <i>spicifera</i> (M. Vahl) Borgesen	R	Competitively superior to native <i>Laurencia nidifica</i> J. Agardh. High abundance at some sites, increasing total algal biomass	O, Sur, E	SM HC	USA (Hawaii)	Russell 1992
<i>Acanthophora</i> <i>spicifera</i>	R	Most common introduced seaweed in Hawaii, common in intertidal and tide pools, displaces native macroalgae (but no data given)	O, Sur	SM	USA (Hawaii)	Smith et al. 2002
<i>Avrainvillea</i> <i>amadelphe</i> (Montagne) A. Gepp et E.S. Gepp	R	Co-occurrence in previously monospecific <i>Halophila hawaiiensis</i> Doty et Stone meadows	O, Sur	CC	USA (Hawaii)	Smith et al. 2002
<i>Bonnemaisonia</i> <i>hamifera</i> Harlot	R	Increase in abundance, now common component of community (24% maximum cover)	O, Sur	SM	USA (Atlantic coast) Gulf of Maine	Harris and Tyrell 2001
<i>Caulerpa</i> <i>filiformis</i> (Suhr) K. Hering	G	Increase in abundance since first record in 1920s to become dominant species in several locations in New South Wales, Australia	O (Serial collections)	SM	Australia (Pacific coast)	May 1976
<i>Caulerpa</i> <i>racemosa</i> (Forsskål) J. Agardh	G	Overgrowth increased shoot density of <i>Cymodocea nodosa</i> (Ucria) Ascherson and decreased shoot density of <i>Zostera noltii</i> Hornem. in mixed meadows	E (removal)	CC	Italy (Med, Tuscany coast)	Ceccherelli and Campo 2002
<i>Caulerpa</i> <i>racemosa</i>	G	Reduced species number, diversity and abundance of native macroalgae	Sur (comp)	CC	Italy (Med, Tuscany coast)	Piazzi et al. 2001a
<i>Caulerpa</i> <i>taxifolia</i> (M. Vahl) C. Agardh	G	Invaded areas: decrease in number, width, and longevity of leaves; health of <i>Posidonia oceanica</i> (L.) Delile. After 3 years of competition, mortality of sparse seagrass beds	Sur (comp)	CC	Italy (Med, Elba)	De Villèle and Verlaque 1995
<i>Caulerpa</i> <i>taxifolia</i>	G	Negative effect on shoot density of <i>Cymodocea nodosa</i> , amplified by nutrient enrichment. In long-term, species co-exist, no influence of nutrients	E (enrichment, removal)	CC	Italy (Med, Elba)	Ceccherelli and Cinelli 1997 Ceccherelli and Sechi 2002

(Table 1 continued)

Species	Summary	Method	Effect	Location	Reference
<i>Caulerpa taxifolia</i>	G Higher density and diversity of invertebrate epifauna and fish in <i>C. taxifolia</i> compared to <i>Cymodocea nodosa</i> meadows species composition changed, mainly <i>Polychaeta</i> on <i>C. taxifolia</i> . Important economic fish species absent in <i>C. taxifolia</i> meadows	Sur (comp)	HT HC	Italy (Med, Ligurian Sea)	Relini et al. 1998a-c, Relini et al. 2000
<i>Caulerpa taxifolia</i>	G Less biomass and diversity of native algal and invertebrate species	Sur (comp)	CC HT	France (Med)	Boudouresque et al. 1992
<i>Caulerpa taxifolia</i>	Diversity higher in non-invaded area (note: Chisholm et al. 1997 also found large difference in water quality, sediment organics and pollution between the two areas)	Sur (comp)	CC	France (Med, Ligurian Sea)	Verlaque and Fritayre 1994
<i>Caulerpa taxifolia</i>	G No evidence of decrease in <i>Posidonia oceanica</i> abundance, <i>C. taxifolia</i> and seagrass patches well isolated, indication of no significant competition	Sur	-	France (Med, Ligurian Sea)	Jaubert et al. 1999
<i>Caulerpa taxifolia</i>	G No clear effect on composition and species richness of ichthyofauna, no change in fish feeding habits, reproduction, recruitment. Fish density and biomass slightly lower in invaded sites	Sur (comp)	HT	France (Med, Ligurian Sea)	Francour et al. 1995
<i>Caulerpa taxifolia</i>	G Colour change of a number of fish species inhabiting <i>C. taxifolia</i> meadows	Sur (comp)	HT	France (Med, Ligurian Sea)	Arigoni et al. 2002
<i>Caulerpa taxifolia</i>	G Biomass of <i>Ruppia maritima</i> L. 20x lower in invaded patches	Sur (comp)	CC	USA (Pacific coast, San Diego)	Williams and Grosholz 2002
<i>Caulerpa taxifolia</i>	G Reduced abundance of invertebrates compared to <i>Zostera marina</i> L.	Sur (comp)	HT	USA (Pacific coast, San Diego)	Tippets 2002
<i>Caulerpa taxifolia</i>	G <i>Caulerpenyne</i> and <i>C. taxifolia</i> extracts inhibit or delay the proliferation of phytoplankton strains	Lab	TO		Merino et al. 1994 (in Boudouresque et al. 1995), Lemée et al. 1997
<i>Caulerpa taxifolia</i>	G Consumption by sea urchins results in impaired gonadal development and loss of spines	Lab	TO		Boudouresque et al. 1996
<i>Caulerpa taxifolia</i>	<i>Caulerpenyne</i> and <i>C. taxifolia</i> extracts inhibit development of sea urchin eggs	Lab	TO		Lemée et al. 1993, Pedrotti et al. 1996, Pesando et al. 1996, Amade and Lemée 1998, Pedrotti and Lemée 1999

(Table 1 continued)

Species	Summary	Method	Effect	Location	Reference
<i>Caulerpa taxifolia</i>	G Caulerpenyne changes behavior of marine ciliate possibly causing mortality	Lab	TO		Dini et al. 1994 (in Boudouresque et al. 1995), Ricci et al. 1999
<i>Caulerpa taxifolia</i>	G Reduced cover and number of native species colonized by one or both <i>Caulerpa</i> species, more pronounced in <i>C. racemosa</i> patches, compared to invaded controls. More <i>Womersleyella</i> in <i>C. taxifolia</i> areas	Sur (comp)	CC	Italy (Med, Tuscany coast)	Piazzi et al. 2003, Balata et al. 2004
<i>Caulerpa racemosa</i>	G Laboratory testing of Caulerpenyne: antibacterial and antifungal properties, sea urchin larval and fish toxicity. Avoidance of treated feed pellets by fish, mortality in molluscs fed with treated algae	Lab	TO		Paul and Fenical 1986
<i>Caulerpa taxifolia</i>	G <i>C. taxifolia</i> extracts and caulerpin from <i>C. racemosa</i> inhibit membrane extrusion pump (protective mechanism against toxins) in mussel and sponge, making sponges less resistant to tributyl tin	Lab	TO		Schröder et al. 1998
<i>Caulerpa taxifolia</i>	G 50–100% cover of benthic macroalgae is introduced; cover and diversity of native species lower in invaded areas. No turf in <i>C. racemosa</i> patches, some <i>W. setacea</i> in <i>C. taxifolia</i> patches	Sur (comp)	CC	Italy (Med, Tuscany coast, harbor area)	Piazzi and Cinelli 2003
<i>Caulerpa racemosa</i>	R Richness and species number of invertebrates (mainly amphipods) slightly reduced in invaded areas	Sur (comp)	HT	France (Med, Ligurian Sea)	Bellan-Santini et al. 1996
<i>Womersleyella setacea</i> (Hollenberg)	G <i>Codium</i> now dominant, establishment only after previous disturbance of canopy-forming kelps, then preventing recruitment of native kelps. Native algal abundance decreased	O, Sur	CC HC	Canada (Atlantic coast, Nova Scotia)	Chapman et al. 2002
R.E. Norris	G <i>Codium</i> now dominant, establishment only after previous disturbance of canopy-forming kelps, then preventing recruitment of native kelps. Native algal abundance decreased. Less abundance of juvenile fish in invaded patches	O, E (removal, herbivory assays), Sur	CC HC HT	USA (Atlantic coast, Gulf of Maine)	Levin et al. 2002
<i>Acrothamnion preissii</i> (Sonder)					
E.M. Wollaston					

(Table 1 continued)

Species	Summary	Method	Effect	Location	Reference
<i>Codium fragile</i> ssp. <i>tomentosoides</i>	G Shift in abundance over 25 years from kelp-dominated to <i>Codium</i> and introduced red algae-dominated plus native opportunistic species [<i>Desmarestia aculeata</i> (Linnaeus) J.V. Lamouroux], but high annual variation	O, Sur	CC HC	USA (Atlantic coast, Gulf of Maine)	Harris and Tyrell 2001
<i>Codium fragile</i> ssp. <i>tomentosoides</i>	G Not preferred by sea urchins, no gonadal development on <i>Codium</i> diet	Lab	HT		Scheibling and Anthony 2001
<i>Fucus evanescens</i> C. Agardh	B Fertile hybrids with <i>F. serratus</i> L.	Lab	G	Sweden (Baltic Sea)	Coyer et al. 2002
<i>Fucus evanescens</i>	B Lower biomass and fewer species of epiphytes and grazers, different epifauna composition and lower abundance of amphipods compared to native species	Sur (comp)	CC HT	Sweden (Baltic Sea)	Wikström and Kautsky 2004, Wikström et al. 2006
<i>Gracilaria salicornia</i> (C. Agardh) E.Y. Dawson	R Increase in distribution, dominant species at some sites	O, Sur, Lab	SM	USA (Hawaii)	Smith et al. 2002, Smith et al. 2004, Conklin and Smith 2005
<i>Heterosiphonia japonica</i> Yendo	R Most common species in sheltered and semi-exposed subtidal (6 to >12 m), overgrowing benthos such as rhodoliths	O, Sur	SM	Norway (North Sea coast)	Husa et al. 2004
<i>Hypnea musciformis</i> (Wulfen) J.V. Lamouroux	R Often epiphytic on introduced <i>Acanthophora spicifera</i> , dominant species at some sites, together with <i>A. spicifera</i> leading to higher total algal biomass on some reefs	O, Sur	SM HC	USA (Hawaii)	Russell 1992
<i>Hypnea musciformis</i>	R Epiphyte on other macroalgal species, forms large monospecific blooms at some sites and/or grows intermingled with dense <i>Ulva fasciata</i> Delile	O, Sur	SM	USA (Hawaii)	Smith et al. 2002
<i>Kappaphycus</i> spp. (as <i>Eucheuma striatum</i> F. Schmitz)	R Higher invertebrate diversity compared to non-invaded reef site, observation of coral mortality after smothering. No competition with native seaweeds, higher total algal biomass at some sites	O, Sur	SM HT HC	USA (Hawaii)	Russell 1983
<i>Kappaphycus</i> species	R Dominant at some sites, dense mats attached to reef substrata	O, Sur	SM	USA (Hawaii)	Smith et al. 2002, Conklin and Smith 2005

(Table 1 continued)

Species	Summary	Method	Effect	Location	Reference
<i>Kappaphycus</i> species	R Overgrowth of reef-building corals, leading to partial mortality	O, Sur	HT	USA (Hawaii)	Woo 2000 cited in Conklin and Smith 2005
<i>Neosiphonia harveyi</i> J. Bailey) M.-S. Kim, H.-G. Choi, Guiry et G.W. Saunders (as <i>Polysiphonia harveyi</i> J. Bailey)	R 100% cover in one location	O, Sur	SM	USA (Atlantic coast, Gulf of Maine)	Harris and Tyrell 2001
<i>Sargassum muticum</i> (Yendo) Fensholt	B Decreased cover and native algal species number under <i>S. muticum</i> stands	O, Sur (comp)	CC	Italy (Med, Adriatic Sea, Venice)	Curiel et al. 1998
<i>Sargassum muticum</i>	B Canopy reduced cover of native species, esp. <i>Laminaria saccharina</i> (L.) J.V. Lamouroux and <i>Fucus vesiculosus</i> L.	Sur	CC	Denmark (Limfjord)	Stæhr et al. 2000
<i>Sargassum muticum</i>	B Increased abundance of native kelp and understory species after experimental removal of canopy. Fewer sea urchins at invaded sites	E (removal), Lab	CC HT	USA (Pacific coast)	Britton-Simmons 2004
<i>Sargassum muticum</i>	B High abundance in tidepools caused decreased abundance of leathery and foliose macroalgae	E	CC	Spain (Atlantic coast)	Viejo 1997
<i>Sargassum muticum</i>	B Sargassum rapidly colonized exp. cleared areas, canopy then decreased recruitment of <i>Rhodomela larix</i> (Turner) C. Agardh	E (removal)	CC	Canada (Pacific coast)	De Wreede 1983
<i>Sargassum muticum</i>	B Most abundant species in lower intertidal and subtidal, decrease of <i>Laminaria digitata</i> (Hudson) J.V. Lamouroux abundance	O, Sur	CC	France (Atlantic coast)	Cosson 1999
<i>Sargassum muticum</i>	B Colonization of areas previously colonized by <i>Zostera marina</i> , no re-colonization by <i>Z. marina</i>	O, Sur	CC	France (Atlantic coast)	den Hartog 1997
<i>Sargassum muticum</i>	B Recruitment after <i>Macrocystis pyrifera</i> (L.) C. Agardh dieback; seasonal <i>S. muticum</i> canopy at high density during peak of <i>M. pyrifera</i> recruitment, inhibiting re-colonization	E (removal)	SM	USA (Pacific coast)	Ambrose and Nelson 1982

(Table 1 continued)

Species	Summary	Method	Effect	Location	Reference
<i>Undaria pinnatifida</i> (Harvey) Suringar	B No detectable effect on native algal assemblage over 3 years	Sur (BACI)	-	New Zealand	Forrest and Taylor 2002
<i>Undaria pinnatifida</i>	B No detectable effect on native algal assemblage	Sur (BACI)	-	New Zealand	Wear and Gardner 1999, (cited in Sinner et al. 2000)
<i>Undaria pinnatifida</i>	B Wellington Harbour: <i>U. pinnatifida</i> subcanopy invertebrate assemblages different, many ascidians, polychaetes and hydroids; accumulation of fine sediment; low cover of <i>Corallina</i> and turfs. Queen Charlotte Sound: increase in subcanopy species diversity (algae, molluscs, echinoderms), possibly because of increased habitat complexity	O, Sur (comp)	CC HT	New Zealand	Battershill et al. 1998
<i>Undaria pinnatifida</i>	B Decreased cover of understory species under 100% <i>U. pinnatifida</i> cover	O, Sur (comp)	CC	Italy (Med, Adriatic Sea, Venice)	Curjel et al. 1998
<i>Undaria pinnatifida</i>	B Decreased species richness and diversity of native seaweeds	E (removal)	CC	Argentina (Patagonia)	Casas et al. 2004
<i>Undaria pinnatifida</i>	B High density of <i>U. pinnatifida</i> after experimental reduction of native canopy, recovery after 2 years, but with changed native community composition	E (removal)	CC	Australia (Tasmanian east coast)	Valentine and Johnson 2003
<i>Undaria pinnatifida</i>	B Establishment of <i>U. pinnatifida</i> at high abundance after dieback of canopy-forming <i>Phyllospora comosa</i> (Labillardière) C. Agardh	Sur (comp)	SM	Australia (Tasmanian east coast)	Valentine and Johnson 2004
<i>Undaria pinnatifida</i>	B High density of <i>U. pinnatifida</i> after experimental removal of native canopy, recovery to near control-level after 1 year	E (removal)	SM	Australia (Tasmanian east coast)	Edgar et al. 2004
<i>Undaria pinnatifida</i> Sargassum muticum	B Dominant component in Venice lagoon, competition with <i>Sargassum muticum</i> assumed	O, Sur	SM	Italy (Med, Adriatic Sea, Venice)	Curjel et al. 2001
<i>Womersleyella setacea</i> <i>Acrothamnion preissii</i>	R Reduced functional diversity of seagrass rhizome epiphytes at sites invaded by turf species compared to unaffected sites	Sur	CC HC	France, Italy, Spain (several sites in W-Med)	Piazzi and Cinelli 2000, Piazzi et al. 2002

(Table 1 continued)

Species	Summary	Method	Effect	Location	Reference
<i>Womersleyella setacea</i>	R Dominant species	Sur	SM	Italy (Med, Ligurian Sea)	Airoldi et al. 1995, Airoldi 1998
<i>Womersleyella setacea</i>	R Species co-occur and compete with one another; overall space monopolization is independent of the respective dominant species	Sur (comp)	SM CC	Italy (Med, Tuscany coast)	Piazzi and Cinelli 2001
<i>Acrothamnion preissii</i>	R				

Methods: field survey (Sur); field survey comparing invaded and non-invaded sites [Sur (comp)]; field survey with temporal comparisons before/after invasion [Sur (BACI)]; field experiment (E); laboratory experiment or assay (Lab); observational study (O).

Impact categories: competition with native biota, subcategories: space monopolization (SM); change in community composition (CC); G=genetic effects; HT=effects on higher trophic levels (HT), subcategory toxicity (TO), habitat change (HC), no significant impact shown (-).

B=brown algae (Phaeophyceae), G=green algae (Rhodophyta), R=red algae (Rhodophyta), Med=Mediterranean Sea.

abundances, or become the dominant benthic species in some locations. It is important to note that case studies of impacts of the above species are available only for small portions of the geographical ranges that have been invaded (see countries or regions marked by an asterisk in the following list):

C. taxifolia, introduced to the: Mediterranean Sea (Croatia; France*; Italy*, Monaco; Spain; Tunisia), NW Pacific Ocean (Japan – failed introduction), NE Pacific Ocean (USA: California*), SW Pacific Ocean (Australia: South Australia, New South Wales).

U. pinnatifida introduced to the: Mediterranean Sea (France; Italy*), NE Atlantic Ocean (Belgium; Netherlands; England; France; Spain), NE Pacific Ocean (USA: California; Mexico: Baja California), Australasia (Australia: Tasmania*, Victoria; New Zealand*), S Atlantic (Argentina*).

S. muticum, introduced to the: Mediterranean Sea (France; Italy*), NE Atlantic Ocean (Belgium; Denmark*, Great Britain: England, N Ireland, Scotland, Wales; France*; Germany; Ireland; The Netherlands; Norway; Portugal; Spain*; Sweden), NE Pacific Ocean (Canada: British Columbia*; USA: Washington and Oregon*; Mexico: Baja California).

C. fragile ssp. *tomentosoides*, introduced to the: Mediterranean Sea (France), NE Atlantic Ocean (Belgium; Denmark; Great Britain: England, N Ireland, Scotland; France; Germany; Ireland; The Netherlands; Norway; Portugal: Azores; Spain; Sweden), NE Pacific Ocean (USA: California and Oregon), NW Atlantic Ocean (Canada: Nova Scotia* and Prince Edward Island, USA: Connecticut, Maine*, Maryland, Massachusetts, New York, North Carolina, Rhode Island), SW Pacific Ocean (Australia: Tasmania, Victoria, New South Wales; New Zealand).

The nature and, where known, the underlying mechanisms of the ecological impacts of these four species are discussed in detail below (also refer to Table 1).

We briefly discuss case studies of red algal introductions to the Hawaiian Islands, a small but well-studied area with a relatively high number of abundant alien seaweeds (N.B.: While the number of alien seaweed species is higher in other areas, e.g., in the Mediterranean Sea, the proportion subjected to impact-related studies is relatively higher for Hawaii).

Caulerpa taxifolia

A large research effort has addressed the ecological impacts of *Caulerpa taxifolia* in the Mediterranean Sea. The presence of *C. taxifolia* had a negative effect on shoot density of the seagrass *Cymodocea nodosa* in short-term studies, especially under nutrient enrichment (Ceccherelli and Cinelli 1997), whereas long-term experiments suggested that the two species are likely to co-exist and that high nutrient availability will not change competitive relations (Ceccherelli and Sechi 2002). In contrast, the dominant seagrass in the Mediterranean Sea, *Posidonia oceanica*, is negatively affected by competition with *C. taxifolia*, leading to decreased productivity and shoot mortality, especially in sparse meadows (De Villele and Verlaque 1995). *P. oceanica* facilitates *C. taxifolia* colonization and growth by providing physical

protection, rather than shade (Ceccherelli and Cinelli 1998, 1999). The distribution and abundance of *P. oceanica* has, however, not changed in the Bay of Menton (French Mediterranean Sea) over 7 years since *C. taxifolia* was introduced; *C. taxifolia*- and *P. oceanica*-dominated areas seem well separated, implying minimal competition at larger geographic scales (Jaubert et al. 1999). Sites on the French Mediterranean coast colonized by *C. taxifolia* typically show reduced biomass and diversity of native macroalgae and invertebrates and low fish abundance (Boudouresque et al. 1992, Verlaque and Fritayre 1994, Francour et al. 1995, Bellan-Santini et al. 1996). In contrast, Italian studies (only about 50 km from the French study sites) report higher biomass and diversity of invertebrates and fish in *C. taxifolia* meadows (presumably as a result of increased habitat complexity), but a significant lack of some important economic species that require open sand habitats (Relini et al. 1998a–c; 2000). Toxic secondary metabolites of *C. taxifolia* had negative effects on sea urchin larvae and protists in the laboratory (Table 1), but whether similar effects manifest in the field is unknown.

Since the early 1990s, a second *Caulerpa* species has been spreading in the Mediterranean Sea, recently proposed as *C. racemosa* var. *cylindracea* (Verlaque et al. 2003). This species was also recently recorded as introduced in a water body in South Australia (Collings et al. 2004). In Italy, overgrowth by *C. racemosa* var. *cylindracea* reduced diversity and abundance of native macroalgae, especially turf and encrusting species (Piazzi et al. 2001a), and in mixed meadows of *C. nodosa* and *Zostera noltii* decreased shoot density of the former species but increased density of the latter (Ceccherelli and Campo 2002). Where they co-occur, *C. racemosa* var. *cylindracea* has higher growth rates and is competitively superior to *C. taxifolia* (Piazzi et al. 2001b, Piazzi and Ceccherelli 2002). Colonization by either species reduced diversity and abundance of native macroalgae compared with uninvaded areas, with *C. racemosa* var. *cylindracea* having the most pronounced effect (Balata et al. 2004). On the Tuscan coast, Italy, the two introduced *Caulerpa* species also interact with two introduced turf-forming red algae, *Womersleyella setacea* and *Acrothamnion preissii* (Piazzi and Cinelli 2003). The four species form a mosaic of largely introduced assemblages, with different species dominating, depending on habitat. Native species abundance and diversity are lower than in uninvaded areas (op. cit.). The introduced turf assemblages also promote growth and spread of introduced *Caulerpa*, whereas areas with a higher complexity and species diversity were less conducive (Ceccherelli et al. 2002). In summary, introduced *Caulerpa* species have monopolized benthos in some areas of the Mediterranean Sea, and through increased competition have caused significant changes to community composition, usually evident as reduced cover and richness of native seaweeds and marine plants.

Impacts of introduced *Caulerpa taxifolia* in other parts of the world are scarcely known. In California, biomass of the seagrass *Ruppia maritima* was 20 times lower in meadow patches colonized by *C. taxifolia* (Williams and Grosholz 2002), and abundance of invertebrates was

lower in *C. taxifolia* patches than in *Zostera marina* meadows (Tippets 2002). Information about impacts in the southern states of Australia is at present primarily anecdotal (Glasby et al. 2005).

Undaria pinnatifida

Undaria pinnatifida populations dominate space in many regions where the species has been introduced (e.g., Sinner et al. 2000, Forrest and Taylor 2002, Hewitt et al. 2005). Manipulative field experiments demonstrate that the establishment of *U. pinnatifida* is facilitated by increased substratum availability created by disturbance (Valentine and Johnson 2003, Edgar et al. 2004, Valentine and Johnson 2004). Once established, it forms predominantly seasonal canopies that act to decrease cover, and sometimes the diversity of understory species (Battershill et al. 1998, Curiel et al. 1998, Casas et al. 2004). However, other studies have detected either no significant differences in diversity or cover of native macroalgal assemblages in invaded versus non-invaded areas (Wear and Gardner 1999, cited in Sinner et al. 2000, Forrest and Taylor 2002) or, more rarely, an increase in subcanopy species diversity (Battershill et al. 1998). Re-establishment of native assemblages after 1 to 2 years has been observed where high abundances of *U. pinnatifida* have been removed by manual clearing (Valentine and Johnson 2003, Edgar et al. 2004), albeit with changed species composition (Valentine and Johnson 2003). Sea urchin grazing can significantly reduce *U. pinnatifida* abundance but not enough to prevent canopy establishment (Valentine and Johnson 2005a). However, *U. pinnatifida* seems not to inhibit recruitment of native understory species (Valentine and Johnson 2005a,b; see also Valentine et al. 2007). At low grazing pressure, *U. pinnatifida* persists while native canopy-forming seaweeds recover poorly, due to build-up of sediment in areas where native canopy-forming species are lost.

Sargassum muticum

Shortly after the discovery of *Sargassum muticum* on the south coast of England, the species was reported to have profoundly altered the coastal ecology, albeit without supporting data (Fletcher and Fletcher 1975). Recruitment and establishment of this species is often facilitated by disturbance creating available substratum (Ambrose and Nelson 1982, Deysher and Norton 1982, Critchley et al. 1987). The seasonal canopy of *S. muticum* then prevents re-establishment of native macroalgae (Ambrose and Nelson 1982, De Wreede 1983) and eelgrass (den Hartog 1997). Reduced abundances and sometimes reduced richness of native seaweeds have been found in invaded areas (Viejo 1997, Curiel et al. 1998, Stæhr et al. 2000, Britton-Simmons 2004). Underwater light measurements support the notion that shading by *S. muticum* is the most likely factor preventing re-growth of native species (Britton-Simmons 2004). The reduced abundance of native seaweeds has led to decreased abundance of the sea urchin *Strongylocentrotus droebachiensis* (op. cit.), which avoids consumption of *S. muticum*, indirectly supporting the persistence of the introduced seaweed.

Codium fragile ssp. *tomentosoides*

Establishment and impacts of *Codium fragile* ssp. *tomentosoides* in the NW Atlantic Ocean have been facilitated by interactions with other introduced species. Periodic overgrazing by sea urchins (Johnson and Mann 1988) provided a disturbance to native seaweeds enabling establishment of *C. fragile* ssp. *tomentosoides* (Harris and Tyrell 2001, Chapman et al. 2002, Levin et al. 2002). Sea urchins (*Strongylocentrotus droebachiensis*) prefer kelp as a food source, only consume *C. fragile* ssp. *tomentosoides* when no other seaweeds are available (Sumi and Scheibling 2005) and have impaired gonad development on a diet of only this species (Scheibling and Anthony 2001). However, more importantly, natural sea urchin/kelp dynamics are disrupted by the spread of the introduced bryozoan *Membranipora membranacea* (Linnaeus), which overgrows kelp blades and leads to reduced growth, defoliation and gap formation in New England and Nova Scotian *Saccharina latissima* (L.) Lane, Mayes, Druehl et Saunders [as *Laminaria saccharina* (L.) Lam.] beds (Harris and Tyrell 2001, Chapman et al. 2002, Levin et al. 2002). *C. fragile* ssp. *tomentosoides* recruits into these gaps and persists by inhibiting recruitment of kelp zoospores, the number of which is possibly further reduced by decreased kelp abundance (op. cit.). Space monopolization by *C. fragile* ssp. *tomentosoides* in this manner has resulted in reduced abundance of native macroalgae and of juvenile fish (Harris and Tyrell 2001, Levin et al. 2002). Ecological impacts of established *C. fragile* ssp. *tomentosoides* in other parts of the introduced range have not been studied. Space monopolization by *C. fragile* ssp. *tomentosoides* does not occur in the NE Atlantic Ocean, and Chapman (1999) suggested that high native floral diversity and grazing pressure prevent high abundances of *C. fragile* ssp. *tomentosoides* in this region. The introductions to the NE Atlantic Ocean occurred more than 30 years earlier than those in the NW Atlantic Ocean (reviewed in Chapman 1999). While changes in abundance are likely to occur over decades, there is unfortunately no information as to whether *C. fragile* ssp. *tomentosoides* in the NE Atlantic Ocean ever attained higher abundances in the past.

Hawaiian macroalgal invasions

At least 21 seaweed species have been introduced to the Hawaiian Islands, both accidentally and intentionally for seaweed aquaculture (Godwin 2001, Smith et al. 2002). Several red algal species (*Acanthophora spicifera*, *Avrainvillea amadelpha*, *Gracilaria salicornia*, *Hypnea musciformis*, *Kappaphycus* spp. and *Eucheuma* spp.) have established at high abundances and are spreading on Hawaiian coral reefs (Smith et al. 2002, Conklin and Smith 2005, G. Zucarello personal communication). These species monopolize space and increase overall macroalgal productivity and biomass on coral reefs (Table 1). Overgrowth of reef-building corals has been observed (Woo 2000, cited in Conklin and Smith 2005). Quantitative assessments of their ecological impacts and competitive relationships between each other and with native benthos are, however, not available. The introduced seaweeds exacerbate the problem of persistent

macroalgal blooms in some locations, e.g., Kaneohe Bay, which began in the 1960s with the establishment of high abundances of the native *Dictyosphaeria cavernosa* (Forsskål) Børgesen after disturbance and chronic nutrient enrichment (Smith et al. 1981). Alien and native bloom-forming macroalgal species now form a mosaic with overall high total algal cover sustained by low and spatially variable grazing rates (Stimson et al. 2001) and supported by sediment nutrient levels that remain elevated (Stimson and Larned 2000).

Economic impacts

Information about economic impacts of alien seaweeds is generally rare, indeed the paucity of estimates of economic values in the marine sector in general has been identified as a significant gap (Colgan 2004). Direct impacts of marine macroalgae are largely unquantified, unlike impacts of macrophytes in freshwater systems. Cases of observed or anecdotal reports of economic impacts, summarizing effects on fisheries and aquaculture due to fouling of nets, ropes, floats and other maritime equipment, are collated in Ribera and Boudouresque (1995), Trowbridge (1998; for *Codium fragile* ssp. *tomentosoides*) and Sinner et al. (2000; for *Undaria pinnatifida*), but there are no quantitative data.

One component of the economic impacts of invasive seaweeds is the cost of rapid response, control and eradication efforts (Table 2). Costs differ widely between reports (Table 2), but in most instances it is not obvious how estimates were calculated, so direct comparisons are potentially problematic. However, detailed breakdowns of costs are reported in three recent studies: Anderson (2005) for *Caulerpa taxifolia* in California, Wotton et al. (2004) for *Undaria pinnatifida* in the Chatham Islands, New Zealand, and Miller et al. (2004) for *Ascophyllum nodosum* (L.) Le Jolis in California (Table 2). The total sum of >US\$ 7.5 million for the containment of *C. taxifolia* in California included immediately available emergency funds (the incursion was considered an environmental emergency similar to an oil spill) to commence the eradication and substantial funds for ongoing monitoring, research and public awareness (Anderson 2005; see also Anderson 2007 for further details on the eradication process). The costs of the successful eradication of *U. pinnatifida* from a sunken trawler in New Zealand were for (failed) salvage attempts (85% of total costs), *in situ* treatment of gametophytes and small-sized sporophytes on the ship's hull (13%) and regular monitoring of the ship's hull and adjacent shoreline (2%), all paid by the vessel's insurer (Wotton et al. 2004). In both cases, there were unquantified costs for involvement of government agencies, local authorities, scientists and other stakeholders.

Impacts on amenity and recreational value can be expected in situations where high abundances of introduced seaweed occur. Removal of beach wrack derived from *Hypnea musciformis* blooms in a coastal town in Hawaii costs ~US\$ 55,000 year⁻¹ (van Beukering and Cesar 2004). The authors also predict a significant long-term economic benefit to the local economy via improved real estate values were the algal blooms controlled, e.g.,

Table 2 Economic costs associated with eradication and control efforts for invasive seaweeds. Where no monetary value was available, an estimate of effort is given.

Species	Summary	Cost/effort	Reference
<i>Ascophyllum nodosum</i>	Eradication by manual removal from small incursion area (total of 174 thalli)	US\$ 4680	Miller et al. 2004
<i>Caulerpa taxifolia</i>	Rapid response, containment and ongoing monitoring of incursion in California, USA (2000–2005)	US\$ 7.6 million over 5 year	Anderson 2005
<i>Caulerpa taxifolia</i> *	New South Wales, Australia, application of sea salt	US\$ 5–23 m ⁻²	Glasby et al. 2005
	Estimated cost to treat all colonized areas (~8 km ²) in the State	US\$ 46 million	
<i>Caulerpa taxifolia</i> *	South Australia, freshwater treatment	US\$ 4 million over 3 years	Neverauskas pers. comm.
<i>Hypnea musciformis</i>	Kihei coast, Maui, Hawaii. Removal of biomass from beaches	US\$ 55,000 year ⁻¹	Van Beukering and Cesar 2004
<i>Kappaphycus</i> spp.	Removal from coral reefs in Hawaii	~2 person h m ⁻²	Conklin and Smith 2005
<i>Sargassum muticum</i>	Manual removal by volunteers (group size unknown)	10–70 kg wet weight trip ⁻¹	Critchley et al. 1986
<i>Sargassum muticum</i> **	Estimated costs for mechanized removal (only applied at experimental scale)	~38 US\$ t ⁻¹ (wet weight)	Hurley 1981 cited in Critchley et al. 1986
<i>Undaria pinnatifida</i> ***	Successful eradication from a sunken vessel at the Chatham Islands, New Zealand (heat treatment and monitoring)	>US\$ 1.9 million	Wotton et al. 2004
<i>Undaria pinnatifida</i> *	Manual removal at experimental scale	>US\$ 23,000 over 3 years (5 person day 800 m ² month ⁻¹)	Hewitt et al. 2005

Original figures were converted to US\$ using exchange rates on 10/09/2006.

Conversion factors used: *1 AU\$=0.76 US\$; **1 GB£=1.88 US\$; ***1 NZ\$=0.66 US\$.

by reduction of nutrient inputs. We were unable to find other estimates of revenue loss caused by incursions of invasive seaweeds, as may arise, e.g., at dive sites that were previously attractions because of their high benthic diversity, or by impacting recreational boating or fishing activities (Critchley 1983).

Estimates are generally unavailable for the indirect costs of invasive or potentially invasive seaweeds. These include associated costs of research and education/extension activities. The New Zealand public good science funding agency, the Foundation for Research, Science and Technology (FRST), has explicitly allocated NZ\$ 1.2 million year⁻¹ (~US\$ 0.8 million year⁻¹) towards marine biosecurity research (C.L. Hewitt personal communication). However, this underestimates total marine biosecurity expenditure of FRST, given significant overlaps in research focused on biodiversity and biosecurity. In the United States, National Sea Grant allocates an estimated US\$ 2.4 million year⁻¹ towards research and outreach associated with marine invasions (C.L. Hewitt personal communication).

Costs of management activities are usually not separated by taxonomic group, except in cases where there is a direct response to a particular invasion. In Australia, the establishment of a National System for the Management of Marine Pests is estimated to cost AU\$ 7 million over the three-year period 2004–2007 (~AU\$ 2.3 million year⁻¹ = ~US\$ 1.9 million year⁻¹; N. Parker personal communication). This total is derived from a combination of appropriation funds within the Commonwealth Government (Department of Agriculture, Forestry and Fisheries, DAFF) and Natural Heritage Trust funding (shared between DAFF and the Department of Environmental Heritage). New Zealand has also recently adopted a Biosecurity Strategy (Biosecurity Council 2003) in which Marine Biosecurity was identified as a priority. As a consequence, the government agreed to a significant investment in enhanced marine biosecurity delivery in the 2004/05 budget, leading to an increase in marine biosecurity expenditure of almost 300% to ~NZ\$ 6.9 million year⁻¹ (~US\$ 4.8 million year⁻¹), representing ~4% of total biosecurity expenditure (Hewitt and Bauckham

2004, Hewitt et al. 2004b). While this is proportionally much less than the economic contribution of primary marine industries to New Zealand's GDP, it is a large improvement over previous investment. The management of marine introduced species in the United States is vested within a large number of Federal and State agencies including the US Coast Guard, US Geological Survey, US Fish and Wildlife Service, and individual State natural resource management agencies. Identifying all expenditure on managing marine introductions is beyond the scope of this review. We were unable to find any quantitative information about societal impacts of seaweed invasions.

Discussion

Our review of available published literature showed that quantitative assessments of ecological and economic impacts of invasive seaweeds are still scarce. The lack of these data, for both marine and terrestrial ecosystems, is generally bemoaned in the invasion biology literature (e.g., Parker et al. 1999, Ruiz et al. 1999, Gurevitch and Padilla 2004). The data are urgently required to adequately inform and guide the management of invasive or potentially invasive species.

The mechanisms underlying impacts of alien seaweeds are uncertain (see Levine et al. 2003 for discussion of this issue for better-studied higher plant introductions). In the majority of reported cases, impacts are typically expressed as community dominance of the invader through monopolization of space, and changing competitive relationships in the native assemblage. However, the mechanisms causing these community changes are mostly unknown (but see Valentine et al. 2007). Impacts of alien species cannot be viewed in isolation from the preceding stages in the invasion process, namely successful establishment and spread (for further discussion see Valentine et al. 2007 and Dunstan and Johnson 2007). These preceding stages and the manifestation of impacts through high abundances and space monopolization reflect characteristics of i) the recipient environment (e.g., disturbance, resource availability, competition and community composition) and ii) the invader (e.g., high growth rates, high fecundity). Closer examination of these two factors and of interactions between invaders may suggest the underlying mechanisms for the observed community changes.

Influence of the recipient environment

The analysis of the invasion history of a species is often used to predict whether that species would become invasive elsewhere, and hence likely to cause negative impacts (Lodge 1993, Williamson 1999, Hayes and Sliwa 2003, Branch and Steffani 2004). However, impacts observed in one location often do not predict the effects in another location, because the factors determining success of establishment and further spread may be site- or time-specific (Grosholz 1996). A good example of this is the significant impact of introduced *Codium fragile* ssp. *tomentosoides* on western Atlantic coasts, compared to

the relatively benign effect of this species on benthic communities in the east Atlantic Ocean (see above, Table 1).

There are indications for a relationship between disturbance, which may lead to resource variability in the recipient habitat, and the establishment of invasive species and their proliferation to high abundances with associated impacts (Davis et al. 2000, Mack et al. 2000, MacDougall and Turkington 2005, Dunstan and Johnson 2007, Valentine et al. 2007). Once established, positive feedback mechanisms can enable invasive seaweeds to persist and flourish, even in the absence of the original disturbance (Valentine et al. 2007). Anthropogenic disturbance leading to changes in resource availability (e.g., high nutrient availability, water and sediment pollution, structures providing artificial substrata and altered temperature regime due to effluents) often leads to higher incidence and abundance of invaders (reviewed in Carlton 1996, Gollasch and Leppäkoski 1999). For example, *Undaria pinnatifida* often forms dense stands on artificial substrata (e.g., Floc'h et al. 1996) and abundant populations of *C. fragile* ssp. *tomentosoides* in Australia are generally found in engineered environments, e.g., marinas, wharfs, jetties, bund walls and riprap (B. Schaffelke personal observations). Highly abundant *Caulerpa taxifolia* has been found on sediments enriched with nutrients and organic matter from urban wastewater, resources which *C. taxifolia* can utilize, whereas uninvaded sites or sites with low invader abundance are less polluted (Chisholm et al. 1997). The less polluted sites also have higher cover of native macrophytes, which may be due to impacts of the invader or the pollution, or both. Extensive blooms of other introduced *Caulerpa* species have also been linked to local nutrient enrichment by sewage inputs, *C. brachypus* var. *parvifolia* Harvey, recently discovered in Florida, and *C. ollivierii* Dostál in the Bahamas (Lapointe et al. 2005a,b). Facilitation of introductions by climate change (Stachowicz et al. 2002) has not yet been demonstrated for introduced seaweeds, although biogeographic limits of many macroalgae are known to be temperature-controlled (Breeman 1988).

Biological interactions also play a major role in controlling high abundances and space monopolization. Recipient habitats with low cover and diversity of native species (either chronically or after acute disturbance) often have a higher incidences and abundances of alien species (e.g., Gollasch and Leppäkoski 1999), although this view has been challenged recently (discussed in Dunstan and Johnson 2007). Nevertheless, low diversity algal turf assemblages and seagrass meadows promoted the establishment of high abundances of introduced *Caulerpa* species in the Mediterranean Sea (Ceccherelli and Cinelli 1998, Ceccherelli et al. 2002) and proliferation of several invading seaweed species is facilitated by reduced native macroalgal cover (see Table 1; and, e.g., Valentine et al. 2007).

Avoidance by herbivores may be an important mechanism that causes shifts in community composition. Control of introduced macroalgal biomass by herbivory is often ineffective, either because invasive seaweeds are not preferred by native grazers (examples in Table 1; *Caulerpa taxifolia*, Boudouresque et al. 1996, Lemée

et al. 1996; *Codium fragile* ssp. *tomentosoides*, Prince and LeBlanc 1992; *Fucus evanescens*, Schaffelke et al. 1995) or preferred by only a few grazers (*C. fragile* ssp. *tomentosoides*, Trowbridge 1995, 1998; *Undaria pinnatifida*, Thornber et al. 2004). However, in some instances no change of herbivores' feeding habits was observed (*C. taxifolia*, Francour et al. 1995).

Role of species' functional traits

Functional traits may influence whether some species are more likely to cause significant ecological or economic impacts. Nyberg and Wallentinus (2005) compared species traits (relating to dispersal, establishment and impact) between European alien and native species. Traits relevant to the manifestation of impacts were size (most invasive green and brown macroalgae were larger than their native counterparts) and growth strategies (invasive species more often form dense covers and inhabit a larger depth range than native species). In that analysis (op. cit.), species most likely to be successful invaders, and hence, likely to have significant negative impacts were *Codium fragile* ssp. *tomentosoides*, *Caulerpa taxifolia*, *Undaria pinnatifida*, *Asparagopsis armata* Harvey and *Grateloupia doryphora* (Montagne) M.A. Howe (currently accepted synonym: *G. turuturu* Yamada, Gavio and Fredericq 2002).

A number of species' traits known from well-studied invader seaweeds are likely to facilitate establishment of high abundances, ultimately leading to impacts. For example, shading by the canopy-forming *Sargassum muticum* was an important mechanism that reduced native biodiversity in invaded areas (Levin et al. 2002). Asexual reproduction and fast growth also have the potential to enable alien seaweeds to quickly colonize available space. However, traits observed in an invasive species are often also found in conspecifics or congeners that are not known to be invasive (Paula and Eston 1987, Trowbridge 1996, Vroom and Smith 2001). Indeed, species' traits alone are unlikely to help predict the likelihood and impacts of invasions (Valentine et al. 2007). Establishment of high abundances more likely depends on characteristics of the recipient environment that result in traits of aliens being advantageous for recruitment and growth, and on sufficient inoculation pressure (Davis et al. 2000, Davis and Pelsor 2001, Dunstan and Johnson 2007, Valentine et al. 2007).

Interactions between invaders

Multiple invasions into one location can synergistically disturb an ecosystem and facilitate the establishment of further alien species – a process that has been termed "invasional meltdown" (Simberloff and von Holle 1999; but see Lohrer and Whitlatch 2002). Examples for facilitation of establishment and growth of one alien seaweed by another is the promotion of *Caulerpa taxifolia* in the Mediterranean Sea by invasive red turf algae (Ceccherelli et al. 2002), and in California by the disturbance of native eelgrass beds by the mussel *Musculista senhousia* (Benson) and the anemone *Bunodeopsis* sp., both of which are alien (Reusch and Williams 1998, 1999, Williams 2002). In the Mediterranean Sea, where two introduced

Caulerpa species co-occur, it is as yet unknown whether *C. racemosa*, which is competitively superior (Piazzi et al. 2001a, Piazzi and Ceccherelli 2002), will eventually replace *C. taxifolia*, or whether the two species will facilitate one another. The outcome of either scenario could be more serious ecological impacts than presently observed. Another example is the facilitation of space monopolization by *Codium fragile* ssp. *tomentosoides* by the invasive bryozoan *Membranipora membranacea*, as discussed above.

Limited inference space

Evidence of impacts of alien marine species is often hampered by the lack of suitable baseline data prior to invasion. Ross et al. (2003) suggest a weight-of-evidence approach to overcome the lack of pre-invasion data, and assessed impacts of a predatory seastar using information from small-scale experimental manipulations, detailed field observations and field surveys at various spatial scales in invaded and uninvaded areas. Such an approach has not yet been applied to assess impacts of seaweed incursions. Typically, studies are only initiated after an incursion has already occurred and use comparisons of sites colonized and not colonized by alien species (see Table 1 for examples). For example, Forrest and Taylor (2002) found no differences in native species richness and abundance due to the establishment of *Undaria pinnatifida* using a control-impact design. However, they suggest that the lack of benthic community data before establishment of *U. pinnatifida* significantly limited their ability to draw inferences. Uncolonized sites may be inherently different from colonized sites, and these differences may have resulted in the lack of the alien species establishment in uncolonized sites, and significant differences in community composition could thus be the result of confounding artifacts. *In situ* experimental introduction of species for impact studies is, typically, deemed unethical and in New Zealand it is illegal. In New Zealand, *U. pinnatifida* is classified as an "unwanted organism" under the Biosecurity Act of 1993, and so it is illegal to disseminate or transport this species. Scientists have tried to circumvent this dilemma through the experimental removal of established invading kelp for comparison with unmanipulated invaded control sites. The manipulated sites are used to simulate species composition in communities that have not been invaded. Results, however, may be difficult to interpret because the experiment may reset the assemblage to an earlier successional stage, which is different from the initial, undisturbed, community (Valentine and Johnson 2003). Re-establishment of native species is possible but full recovery may take several years (Valentine and Johnson 2003, Edgar et al. 2004) and may be impaired by the lack of native species in the immediate vicinity to provide for sufficient recruitment of spores.

Known impacts of other species are limited mostly to single studies at small geographic scales, making comparisons difficult, and inferences about common patterns impossible. The impact studies assessed here cover only a small part of the introduced distributional range for even the best-studied introduced seaweeds (see above).

Caulerpa taxifolia is the one introduced seaweed for which ecological impacts are well documented (Table 1). The majority of studies, however, are from two highly urbanized coastal regions in France and Italy, where *C. taxifolia* reaches very high abundances (see Table 1), and where impacts are most likely. Interestingly, contrasting results were found (see above and Table 1).

Most alien marine species are found in the coastal zone (Carlton 1996), and urbanized embayments, estuaries and ports are considered to be "hot spots" of introductions (Hewitt and Martin 2001, Ruiz and Hewitt 2002, Hewitt 2003a). While environmental disturbance facilitating establishment of aliens may be greater in these environments, they also have a high inoculation pressure, i.e., one or more significant introduction vectors are generally present (Ruiz et al. 2000, Hewitt 2002, Ruiz and Hewitt 2002, Hewitt et al. 2004a). It is debatable whether reported impacts are inherent, species-specific consequences or whether they would be manifested only in disturbed environments. There is also some dispute about how much area of the Mediterranean Sea is colonized by *C. taxifolia*, and hence possibly impacted. Meinesz et al. (2001) estimated a colonized area in the Mediterranean of 131 km², whereas remote sensing results suggest that *C. taxifolia* cover along the south coast of France may have been overestimated by a factor of ten (Jaubert et al. 2003).

Impacts of invaders may also change through time. However, most impact studies are conducted over periods ranging from only weeks to at most a few years, and there is currently no quantitative information about invasive seaweed abundances or impacts on decadal or longer time scales. Long-term monitoring of *Caulerpa taxifolia* in the Mediterranean Sea (Meinesz et al. 2001, Meinesz 2007) is focused on tracking the distribution and spread of this invader, but does have limited abundance or impact information for specific sites. However, this monitoring indicates that areas of highest cover and colonized area are close to the initial incursion point (along the Ligurian coast) and that the spread of *C. taxifolia* is not slowing down. Observations of *Codium fragile* ssp. *tomentosoides* in the Mediterranean Sea and off the coast of Maine (USA) indicate that this species peaked about a decade after first discovery and then declined (reviewed in Trowbridge 1998). However, the reasons for this are unknown. For example, herbivore preferences may change over time from native to alien seaweeds, reducing invader abundance, and alleviating impacts (Stimson et al. 2001). In contrast, invading marine species often persist at low levels and later start to increase in abundance and spread, which Stockwell et al. (2003) attribute to either an initial period of adaptation or a change to previously functional environmental controls such as competition or herbivory. Other reasons may be density-dependent thresholds in survivorship or exponential growth after a lag phase.

Even though rhodophytes are the most prevalent group of alien macroalgae (Ribera Siguan 2003), ecological impacts of this group are known from only a handful of species, mainly those introduced to the Hawaiian islands (Table 1), and are possibly underestimated. Rhodophytes are often inconspicuous and difficult to identify

to species level, there may have been separate introductions of morphologically dissimilar generations (e.g., gametophytes vs. tetrasporophytes of *Asparagopsis armata*, Maggs and Stegenga 1999), or cryptic invasions of sibling species that are morphologically indistinguishable from previously introduced species or native species (e.g., McIvor et al. 2001, Booth et al. 2007). The wider ecological consequences of genetic effects of seaweed invasions (the only example we found is the formation of fertile hybrids between the native *Fucus serratus* and the alien *F. evanescens*; Coyer et al. 2002) are currently unknown.

Economic impacts

The data are too limited to even roughly assess the economic impacts of invader seaweeds. An economic assessment of the impacts of seaweed invasions should cover all potentially affected values including use and non-use values (Perrings et al. 2002, Born et al. 2004, also see Nunes and van den Berg 2001 for a review of economic valuation of biodiversity). The economic costs of species invasions must also include other societal costs such as management and research. We have presented figures for a limited set of countries. However, it is impossible to identify the proportion of these expenses that apply to seaweed invasions only.

We have indications of some costs involved with seaweed invasions, e.g., costs for eradication and control (Table 2). Other costs (e.g., for de-fouling of maritime structures) are perceived to be ongoing costs regardless of the presence of introduced species (Sinner et al. 2000). Even though costs for vessel maintenance (i.e., hull antifouling) are significant for commercial and recreational shipping sectors, they are unusually not considered to be specific to alien marine species (Hassall & Associates Pty Ltd. 2002). The management regimes currently under consideration for hull fouling in Australia and New Zealand may lead to specific, and alien marine species-associated additional costs of maintenance. However, the use of tributyltin in antifouling paints will be phased out globally by 2008 and costs of hull maintenance may increase.

Aquaculture imports and transfers are the main vectors for invading seaweeds in Europe (Ribera Siguan 2002, Wallentinus 2002, Hewitt et al. 2007, Pickering et al. 2007). The ICES Code of Practice for the Introductions and Transfers of Marine Organisms (updated 2003, available at <http://www.ices.dk>) prescribes quarantine and disinfection procedures to alleviate this pathway; however, the costs of compliance with the Code are unknown.

The potential for harvest of commercially valuable seaweeds, either accidentally or intentionally introduced, is generally viewed as a positive impact (see Pickering et al. 2007, for detailed information about intentional seaweed introductions). Invasive *Undaria pinnatifida* is harvested commercially in Australia (Tasmania) and, at least briefly, in Spain (Cremades 1993, cited in Wallentinus 2002). A commercial harvest policy is in place in New Zealand. The species has been cultured in France since 1983, albeit with limited success (Ribera and Boudour-

esque 1995, Fletcher and Farrell 1999). In Argentina this species was first considered to be a new resource (Casas and Piriz 1996), but is now rather viewed as an ecological and economic threat to native seaweed resources (Casas et al. 2004). Introductions of seaweeds for aquaculture are common practice, especially of tropical carrageenophytes (Zemke-White 2004). Impacts of these introductions are poorly understood and are inferred from knowledge about impacts from red algae introduced to Hawaii for aquaculture trials (see Table 1 and Smith et al. 2002). A quarantine protocol for introductions of tropical seaweed has been established, targeting epiphytes and epifauna (Sulu et al. 2003); however, costs for these quarantine measures are unknown. The risks of intentional seaweed introduction have not yet been evaluated with cost-benefit analyses, and such analyses would be difficult to perform currently due to lack of data about impacts. The potential of future introductions of genetically modified seaweeds for aquaculture may add another dimension of uncertainty to this issue.

Management of impacts

Prevention of impacts is the driving force for costly surveillance, eradication and control programs. Managing the impacts of introduced seaweeds goes hand in hand with management strategies aimed at preventing new introductions in the first place and at controlling or eradicating established invading species (Hewitt 2003a, Hewitt et al. 2004b). Clearly, impacts will be avoided if species are prevented from arriving through a range of pre-border management options (op. cit.). Similarly, impacts are likely to be minimized if eradication/control measures are in place to limit the establishment and/or prevent high abundances of established invasive species [for a description control measures for invading seaweeds see Wotton and Hewitt (2004) and Anderson (2007)].

Research needs

Biological invasions have human causes and consequences (Perrings et al. 2002, Hewitt 2005). Future research on impacts of alien seaweeds (and other alien marine species) should focus on multidisciplinary research with biological, social and economic approaches. As impacts are intricately linked to the transport and establishment of alien marine species, much more knowledge is needed about the mechanisms involved in these preceding two stages of the invasion process. Frameworks need to be developed to better predict which species are likely to invade which habitats. The mechanisms that lead to high abundances of introduced seaweeds need to be identified, including the role of anthropogenic disturbance and climate change as confounding factors. The spatial and temporal variability of impacts need to be explored, which will improve the understanding of ecosystem vulnerability and adaptation. This knowledge will support implementation of Article 8h of the Convention of Biological Diversity (prevention, control and eradication of introduced species which threaten ecosystems or species). Without the capacity to measure and predict impacts of alien marine species,

scarce funds for research and management are unlikely to be allocated where they are most needed.

Conclusion

We were unable to find sufficient substantial quantitative information about the impacts of alien seaweeds to detect common patterns. Even though a number of studies have shown significant ecological impacts, the underlying mechanisms are largely unidentified and impacts may be specific to the invaded system or the period of time since establishment and/or past disturbance. In addition, knowledge about socio-economic impacts is extremely scarce. Currently, decisions about management of alien invasive seaweeds are mostly unsupported by best science. Until we are able to understand, predict and measure impacts of alien seaweeds on various spatial and temporal scales, the management of species incursions needs to remain focused on early detection, rapid response and control to reduce the likelihood of impact manifestation.

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