Chapter 12
Invasive Marine Seaweeds: Pest or Prize?

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12.1 Introduction

In recent decades, nonindigenous marine species (NIMS) have become noticeable features of coastal ecosystems worldwide as well as a major environmental problem and a symptom of global change (e.g., Rilov and Crooks 2009; Sellers et al. 2010). The accelerated occurrence of new marine invasions is a function of intensified maritime traffic, coupled with changing environmental conditions in the "recipient" ecosystems. The latter factor may improve the competitiveness of new arrivals in well-established native communities. Transport by ships is the major vector moving marine biota around the globe, mainly via ballast tanks and biofouling on ships' hulls (Flagella et al. 2007). However, the long-range movement of NIMS is also associated with other marine industries such as aquaculture, fisheries, and marine tourism (Hewitt et al. 2009a; Minchin et al. 2009). Global climate change and other regional stressors such as overexploitation of marine resources, marine habitat fragmentation, and coastal pollution are altering the "recipient" ecosystems. This may provide both available space and a suitable ecophysiological window for survival and establishment of NIMS outside the species' native distribution range, or may reveal species' biological traits that are responsible for "invasiveness." Unfortunately, modeled estimates indicate that the rate of biological introductions will continue to increase, in proportion with increasing global trade and economic development (Lin et al. 2007; Meyerson and Mooney 2007). Now and in the future, a major challenge will be to achieve improvements in (1) the early detection of NIMS, (2) the prediction of ecological and socio-economic impacts, and (3) environmental policy and management to prevent new and to control established introductions of NIMS (Lodge et al. 2006; Costello et al. 2007; Rilov and Crooks 2009).

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Macroalgae represent approximately 20% of the world's marine introduced species. High-profile seaweed taxa such as *Caulerpa taxifolia* (Vahl) C. Agardh, *Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (Van Goor) Silva, *Sargassum muticum* (Yendo) Fenshold, and *Undaria pinnatifida* (Harvey) Suringar have led to well-documented economic and ecological consequences in their introduction range (Schaffelke et al. 2006; Schaffelke and Hewitt 2007; Williams and Smith 2007). Following establishment, these species are able to directly affect the habitat profile by monopolizing space and acting as ecosystem engineers and can significantly modify the composition of local communities by altering competitive interactions and trophic networks (Wallentinus and Nyberg 2007).

Terms such as "pest" or "invasive" are often used to describe introduced taxa. A "pest" has been defined as an introduced species with a documented negative economic effect (Williamson and Fitter 1996), while an "invasive species" spreads rapidly from its point of introduction and becomes highly abundant (Kolar and Lodge 2001). In this book chapter, we mainly use the term "invasive" because the economic consequences, and hence the pest status, of an introduced species are generally not well understood (reviewed in Schaffelke and Hewitt 2007).

Global climate change plays a pivotal role in the perpetuation and evolution of organisms and populations, for example, by slowly changing ecological niches and triggering evolutionary events at the species and population levels (Howden et al. 2003; Mainka and Howard 2010). However, it is difficult to predict how climate change will influence species introductions in the near future (Occhipinti-Ambrogi 2007). For instance, changes in environmental conditions may turn a species into an invasive species in its introduced or even in its native range by revealing certain biological traits of that species that were previously not expressed and confer invasiveness (Mueller and Hellmann 2008; Willis et al. 2010). Conversely, environmental changes may decrease the suitability of the ecosystem for newly established or even well-adapted invasive marine species (Mainka and Howard 2010). Although population growth and dispersal potential can be modeled, it is nearly impossible to predict whether a newly introduced species will become invasive, or where and when.

12.2 Biological Traits of Invasive Seaweeds

Seaweeds are good candidates for becoming invasive given their potential to survive long-range relocations via maritime transport (Flagella et al. 2007; up to intercontinental scales; see also Chap. 17 by Rothhäusler et al.) and because many species have a set of biological traits that make them highly competitive. Functional traits that are recognized to facilitate successful invasions include:

1. High growth rates and in some cases large individual sizes (most invasive green and brown macroalgae are larger than their native counterparts)
2. Vegetative propagation (e.g., red and green invasive macroalgae such as *Kappaphycus* sp., *Ulva* sp., *Caulerpa* sp.)
3. Spectacular growth strategies (e.g., invasive species such as *Caulerpa* spp. form dense covers of siphonous single-cell individuals several meters long and inhabit

a larger depth range than native species; canopy-forming *Sargassum muticum* reduces native biodiversity in invaded areas)
4. High levels of sexual reproduction and high fecundity (e.g., in the invasive lineage of *Asparagopsis taxiformis*)
5. Parthenogenetic reproduction and broad environmental tolerances (*Codium fragile* ssp. *tomentosoides*)

A quantitative ranking of European introduced and native seaweed species (using comparisons of categories of biological traits such as dispersal capabilities, environmental tolerances, reproductive mode, and size) indicated clearly that introduced species with a number of these biological traits have an increased likelihood of being a successful invader (Nyberg and Wallentinus 2005). In some cases, however, the biological traits identified in important invasive seaweeds are also present in noninvasive co-specific or co-generic relatives (Paula and Eston 1987; Trowbridge 1996; Chapman 1999; Vroom and Smith 2001).

Rapid micro-evolutionary changes are common in invasive species because introduced populations are often subject to founder effects and population bottlenecks, have higher incidence of hybridization (suggested to provide innovative genetic variants), and are exposed to a range of novel selective pressures encountered in the introduction range (Brown and Marshall 1981). Acclimatization, adaptation, and thereafter phenotypic modification may arise in response to new biotic (e.g., competitors, consumers, or parasites) and environmental conditions and the drivers of the functional changes are likely to be genetic (reviewed in Whitney and Gabler 2008). However, the question remains whether well-established gene regulation mechanisms, already present in the genome's background, are simply activated by the local selective pressure or the aforementioned changes are the result of a de novo genomic response.

Published accounts suggest that only a limited number of biologically distinct species within algal orders or just one ESU (evolutionary significant taxonomic unit); among a number of cryptic ESUs within the same morpho-species become suddenly invasive. In plants, the switch to invasiveness has been recently related with differences in ploidy levels suggesting that genetic attributes such as polyploidy and high chromosome counts may be the drivers for this transformation (endangered plants exhibit disproportionally low levels of ploidy and chromosome numbers compared to invasive plant species; Pandit et al. 2011). Similar to hybridization, polyploidy may lead to the production of novel and greater numbers of genetic variants, which increases the probability of a successful invasion. An association between polyploidy and invasiveness has been reported in the red alga *Asparagopsis taxiformis* (Andreakis et al. 2007b, 2009) and should be further explored in other invasive marine algae, given the general propensity for polyploidy in seaweeds (based on nuclear genome size estimates; Kapraun 2005).

It has been debated whether ecosystems exhibiting high species richness are less vulnerable to biological invasions because in theory only a limited, highly specialized, number of empty niches are available for the invader. Furthermore, it has been assumed that polluted "recipient" environments are likely to promote invasive traits in NIMS (Davis et al. 2000; Davis and Pelsor 2001; Dunstan and Johnson 2007; Valentine et al. 2007; Whitney and Gabler 2008). In addition, invasion attempts are more likely to be successful when the environmental conditions in recipient ecosystems are similar to conditions in the ecosystem the invader has evolved. In the latter case, the chances of survival and establishment of invasive seaweeds following introduction are often improved because their natural enemies such as herbivores or parasites are not introduced with them (i.e., the enemy release hypothesis; Cacabelos et al. 2010; Engelen and Henriques 2011). This means that the energy invested into defense in their native environment (e.g., grazing resistance; see Chap. 8 by Iken) can now support growth and biomass production, increasing the competitiveness of the introduced species.

For a successful invasion, biological traits such as broad ecophysiological tolerance and the consequences of differential gene expression are likely to act in synergy under sufficient inoculation pressure and favorable characteristics of the "recipient" ecosystem. The relative importance of each of these traits, however, is poorly understood because they are likely to be species and location-specific and it is impossible to perform controlled experiments at large biogeographic and evolutionary timescales (Schaffelke and Hewitt 2007).

12.2.1 Seaweed Invasions Are Mostly Human-Mediated

The introduction of a seaweed species often comprises a plethora of immigrants of several genetic variants and ecotypes entering the "recipient" environment. Simplistically, settlement and establishment will be feasible if the species' ecophysiological limits for survival match the environmental conditions in the "recipient" environment. While not fully understood for many individual species, the stages of a successful seaweed invasion have been described as: (1) uptake and transport of propagules, (2) survival and release of propagules and establishment of low-density populations, and (3) increased competition with native biota, spread, expansion, and impact of populations of introduced seaweeds (Schaffelke et al. 2006).

The accidental uptake, transport, and release of propagules into the recipient environment are the only stages of the process when human intervention can prevent biological invasions. Marine seaweeds make use of many vectors for dispersal such as specialized floating structures (see Chap. 17 by Rothäusler et al.), gametes or spores for sexual reproduction, fragments of thalli for vegetative propagation, or attachment to long-distance moving organisms (e.g., sea turtles). The dispersal of most invasive seaweeds, however, is associated with human activities, which could be managed (Hewitt et al. 2009a). Biofouling (i.e., the attachment of the seaweed to any part of a vessel or marine equipment) is one of the most common and also oldest mechanisms of human-mediated relocation of seaweeds. The other main vectors are ballast waters, used to stabilize large vessels for long-distance voyages, that transport algal propagules and intentional relocations of aquaculture species (e.g., as fouling on oyster shells or as packing material) consequently responsible for seaweed introductions (Hewitt et al. 2006).

12.3 The Identification of Introduced Seaweeds Is Not Always Easy

Seaweeds have circumnavigated the globe for centuries. Unintentional introductions by humans have occurred since the beginning of naval explorations and this may explain a perceived "cosmopolitan distribution" reported in many "hull-fouling" species (mostly small, ephemeral species that colonize ship's hulls; Godwin 1975; Ruiz and Carlton 2003). A species' geographic distribution can be misinterpreted especially in taxa with few diagnostic morphological characters (e.g., *Ulva lactuca* Linnaeus, *Bryopsis plumosa* (Hudson) C. Agardh) for the following reasons: firstly, most seaweed taxa have been described from a limited number of geographical regions and/or expeditions; taxonomists in the past relied heavily on these already characterized "type species" to identify new taxa. Secondly, although molecular tools are today able to characterize genealogically distinct units, a significant number of taxonomists still rely on the use of morphological characters for a routine identification of species (Sherwood 2007).

The identification of even well-studied introduced seaweeds is not always straightforward and the assessment of an introduction episode is extremely complex. We will discuss here two important reasons. (1) Due to extreme phenotypic plasticity of many seaweed genera, closely related algal species can be morphologically almost identical and therefore difficult to distinguish. Furthermore, cryptic species with separate geographic distributions have been observed within morphologically homogeneous taxa. Cryptic invasion episodes may therefore occur and are likely to lead to (a) misidentified biologically distinct invasive species due to morphological similarities with natives or (b) misidentified genealogically distinct lineages of invasive character found within a single morpho-species complex. Although forensic techniques may provide the necessary tools to achieve a reliable and quick identification of the invader, results are often compromised by the absence of sufficient DNA sequence data for comparisons and species identification (Box 12.1), even in some phylogenetically important groups of seaweeds (e.g., *Ulva* and *Bryopsis*). Furthermore, a species concept to describe the taxonomical units within these groups is often nonexistent. (2) A large number of species are today recognized as "cryptogenic" (i.e., there is no reliable evidence to indicate whether a species is native or introduced, Carlton 1996); because human-mediated relocations of marine biota have occurred since historical times while archeological or paleontological evidence related to the geographical origins of many soft-body marine organisms is largely absent. A number of biogeographical criteria have been proposed to distinguish between native and introduced taxa (Geller et al. 2010) and a species' cryptogenic history can be resolved in some cases where biological invasions have been systematically studied, e.g., *Ulva flexuosa* Wulfen cited as *Enteromorpha lingulata* J Agardh, *Caloglossa leprieurii* (Montagne) G. Martens, *Bostrychia radicans* (Montagne) Montagne in southern Brazil (Neves and Rocha 2008).

The effective management of a biological invasion requires a solid knowledge of (1) which species has been introduced, (2) the source of the introduction, and (3) the

Box 12.1

Two main approaches are used to identify the source of NIMS. The first relies on the assumption that the vector of introduction (e.g., ballast waters of cargo ships along a specific route) is known. Knowledge of the target species' distribution range and the navigation routes can be combined to identify the likely source regions for that species. Vector management can then prevent further introductions (Ruiz and Carlton 2003). Most importantly, biogeoclimatic models can forecast potential zones vulnerable to invasion and predict the range expansion of invasive NIMS by combining information gathered from species distribution, transport vectors, local ecophysiological conditions, and the species-known ecophysiological tolerance ranges (Arrontes 2005).

A second method deploys DNA sequencing markers and geographical information (phylogeographic approach). Specimens are collected, DNA is extracted, and the same (one or more than one) DNA region is sequenced from multiple individuals to infer the genealogical relationships among introduced and putative native populations of the invasive species and reconstruct the spatial history of the invasion (Fig. 12.1). A variety of DNA sequencing markers have been today developed from mitochondrial, plastid, and nuclear genomes (see case studies); however, the successful use of the approach relies on the resolution of the marker and an adequate sampling strategy. Less applied in seaweed invasion biology is the population genetic approach based on allele frequencies of microsatellite markers to assign individuals to a specific population (for reviews of both approaches, see Wares et al. 2005; Muirhead et al. 2008).

extent of the introduced range. This information can be immediately available where algal floras are well described and survey programs for early detection are in place (Anderson 2007). In geographical regions, however, where local seaweed species are poorly explored and historical records such as species lists are limited, a presumably introduced species may either be native or cryptogenic. Visual surveys and identifications based on gross morphology are often sufficient to detect introductions since many NIMS are conspicuous and genetic discontinuities do not always occur within species (O'Doherty and Sherwood 2007; Castelar et al. 2009). However, many algal genera have extreme levels of phenotypic plasticity and species can potentially hybridize with close relatives (e.g., introduced and native populations of *Fucus evanescens* and *F. serratus*; Coyer et al. 2007). For many introduced seaweeds only multidisciplinary approaches, which take into account molecular, morphological, reproductive, and ecophysiological evidence, are able to characterize the introduced taxonomic units. Such approaches provide sound information on the origins and the geographical trajectory of the invasion and are able to predict persistence and expansion potential of introduced populations (Flagella et al. 2010; Pang et al. 2010).

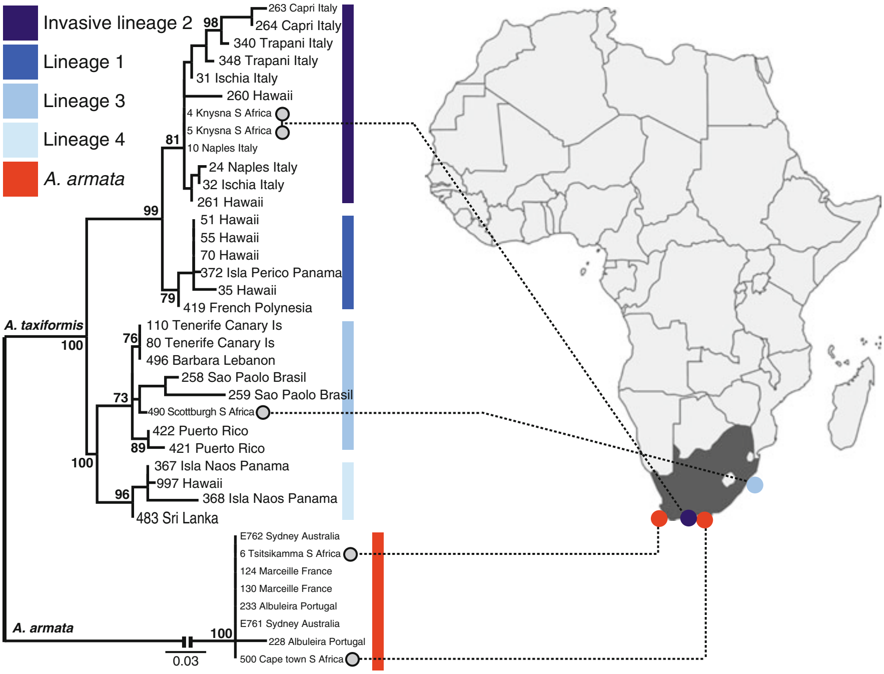

Fig. 12.1 Molecular phylogeographic approach modified from Bolton et al. (2011) to elucidate multiple cryptic introductions of morphologically nearly identical lineages and species (gametophytes and tetrasporophytes) of the red seaweed genus Asparagopsis from specimens collected in South Africa. Both the Indo-Pacific lineage 2 of *A. taxiformis* and *A. armata* constitute notorious invasive species. The highly informative mitochondrial *cox*2–3 intergenic spacer has been deployed in this case. Sequences from previously identified specimens belonging to the five ESUs, collected worldwide and of known origin, are merged with sequences from specimens collected in the study area (*gray circles*) to produce a robust phylogeny and reproduce the two-species genealogical history. From the latter, the identity of each of the target cryptic specimens is revealed. The superimposed geographical information on the phylogram will indicate "which target ESU is where." The level of sequence similarity between sequences of known geographical origin and the target sequences will indicate the source population. Following analyses, unclassified specimens (*gray circles*) are successfully identified (*colored circles*) at the species and lineage levels; lineages and species are finally associated with a geographical location

12.3.1 Relevant Taxonomic Units in Seaweeds Molecular Ecology

Levels and patterns of local marine biodiversity fluctuate, in part due to the exchange of biota among bioregions. In recent years, however, remarkable changes in biodiversity have been revealed at the subspecies level. Molecular techniques in algal systematics are critical to define new relevant units of biological organization for ecological surveys and biodiversity estimates (Box 12.1). These taxonomic units in the vast majority of the cases do not correspond to the traditional species concept (Biological species concept; sensu Mayr 1942) but are recognized within molecular phylogenies as genetically distinct, statistically robust, reciprocally monophyletic clades (Evolutionary Significant Units, ESUs, sensu Moritz 1994; Wattier and Maggs 2001; Provan et al. 2005; Uwai et al. 2006a; Stam et al. 2006; Andreakis et al. 2007a; Verbruggen et al. 2007). The condition of monophyly represents a key assumption for biological classification of organisms; monophyletic clades herein include an organism and all its descendants. ESUs may correlate with geographical distribution and common morphology. Overall, ESUs respect the phylogenetic species concept and are characterized by distinct evolutionary trajectories although the possibility of interbreeding is not excluded.

In the context of invasion biology, ESUs are intended as suitable taxonomic units to elucidate invasions and represent terms such as strains, haplo-groups, lineages, or varieties, conventionally used to express the level of genetic variation and explain the phylogeographic patterns found in introduced seaweeds. The number of uncovered ESUs can vary significantly between studies and largely depends upon the resolution and the speed of “lineage sorting” of the molecular marker used. This is because molecular marker systems are characterized by variable levels of evolutionary speed, distinct genealogical trajectories, and/or uneven intensities of selective pressure; these are all characteristics accounting for the heterogeneity in a phylogenetic signal and its resolution. Therefore, independent information for more than one DNA region and ideally from distinct genomes (nuclear, mitochondrial, and plastid) is necessary to achieve consistent results for delineating ESUs and inferring phylogenies at the sub-species level.

In the last decades, DNA barcoding has been largely used in plant and animal systematics. The method involves sequencing and similarity analysis of a short fragment of DNA from multiple specimens, corresponding to a highly conserved region in the genome such as the subunit one of the mitochondrial gene cytochrome *c* oxidase (COI; Blaxter 2003). However, information coming from a single, extremely short DNA region, compared to the size of a genome, is far from being reliable in modern phylogenetics. This is particularly true in (1) groups of organisms with limited sequence diversity, (2) recently diverged species, (3) hybrids (i.e., offspring of parents belonging to biologically different species, and (4) pseudogenes (i.e., nonfunctional DNA sequences resembling functional genes). The need to employ in a single assay more than one universal biological marker in organism classification can today be satisfied by the increasingly growing number of completely sequenced prokaryotic and eukaryotic genomes. At present, techniques such as DNA microarrays or DNA chips represent the most powerful way to gather as much information as possible from a single individual genome in a single trial in a cost-effective way. In the future, the latter techniques and improvements therein, in combination with advances in data processing and computation power, will permit the inference of phylogenetic relationships among taxonomically robust taxa, ideally at the whole-genome level based on the analysis of their full set of genes (Garzon and Wong 2010).

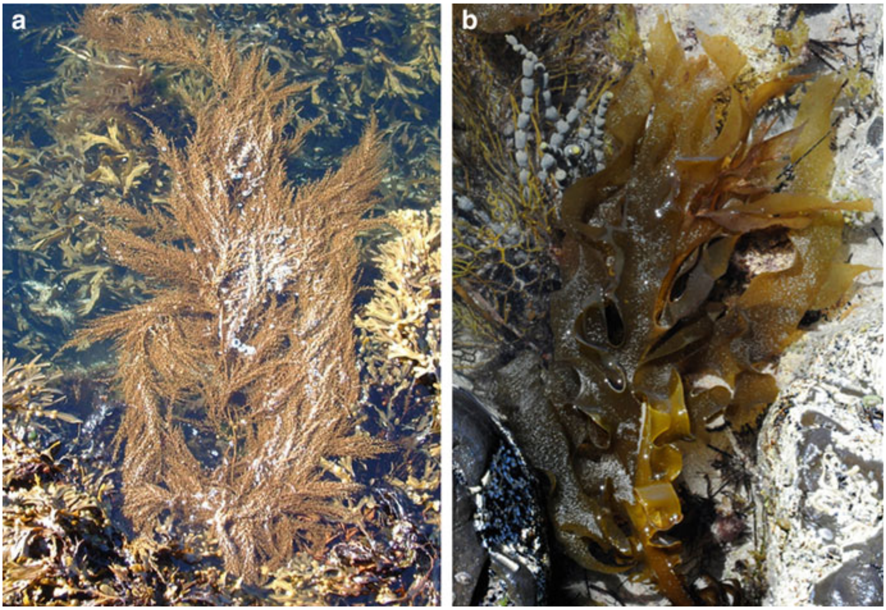

Fig. 12.2 (**a**) *Sargassum muticum* (photo by Stefan Kraan); (**b**) *Undaria pinnatifida* (Harvey) Suringar (Algaebase, image Ref. 15830, photo by Mike Guiry)

12.3.2 Case Study: Sargassum Muticum

The large brown Japanese seaweed *Sargassum muticum* (Yendo) Fensholt (Fig. 12.2a) is one of the most invasive and widely established algae in Europe and North America (Monteiro et al. 2009; Kraan 2008). Contrary to other brown macroalgae (such as *Undaria pinnatifida* and *Fucus serratus*) no evidence for genetic differentiation has been detected between native Asian and introduced populations in this species. This indicated a number of recent invasion events supported mainly by the transport of Pacific oysters introduced for farming in Canada, UK, and France. Nuclear (ITS2; internal transcribed spacer 2) mitochondrial (*Trn*W-*Trn*I spacer) and plastid (RUBISCO spacer) markers failed to uncover significant levels of DNA polymorphisms in *S. muticum* individuals collected globally, which would be required for the reconstruction of the genetic identity of invasive and native populations in this species. The low levels of genetic variability encountered in the native and introduced range of *S. muticum* together with previous morphological confusions with closely related species prohibited the identification of the source populations and the direction of the introduction episodes along the invasion pathway of this important invasive seaweed (Cheang et al. 2010).

12.3.3 Case Study: Undaria Pinnatifida

The brown seaweed *Undaria pinnatifida*, known as the edible *wakame* (Fig. 12.2b), was originally endemic to Japan, Korea, and China where it is industrially cultivated. Firstly observed outside its native distribution range in the Mediterranean Sea (Etang de Thau, French, 1970s) the species has in few years invaded many of the world's oceans from Europe to North America, Australasia, and New Zealand; both by accidental translocation via oyster farming from Japan and intentional introduction for cultivation purposes (Voisin et al. 2005). It was possible to explore and elucidate the invasion history of this species by means of sequence analysis of the mitochondrial *atp*8-*trn*S and *trn*W-*trn*I intergenic spacers, the partial *cox*3 gene and the *tatC-tLeu* gene regions. The latter DNA loci revealed highly differentiated populations, each characterized by low levels of haplotype diversity in the native geographical range of the species (Voisin et al. 2005). On the contrary, where *U. pinnatifida* has been introduced, populations were found to be highly diverse. The so distributed genetic diversity clearly indicated that introduced populations of *U. pinnatifida* are the results of multiple introduction events from more than one native population. Furthermore, the difference in haplotype diversity found in introduced populations sampled from Europe and Australasia indicated differences in the dynamics of the colonization process (Voisin et al. 2005; Uwai et al. 2006a, b).

12.3.4 Case Study: Asparagopsis Armata

The red seaweed *Asparagopsis armata* Harvey (Fig. 12.3a) is a genetically homogeneous species originally described from Southern Australia, Tasmania, and New Zealand and first reported in the northern hemisphere from Algeria in 1925 (Horridge 1951). Molecular phylogenies inferred from the D1, D2, and D3 hyper-variable domains of the nuclear large subunit rDNA gene the plastid RUBISCO spacer and the mitochondrial cox2–3 intergenic spacer indicated just a single plastid haplotype distributed worldwide and a limited number of panmictic nuclear and mitochondrial haplotypes in presumably native and introduced populations. *Asparagopsis armata* exhibits great dispersal potential due to a free-floating tetrasporophyte in its life cycle (see below) and propagation via fragmentation and attachment to other floating structures and has always been reported as a recently introduced, potentially invasive, species from the Mediterranean Sea and western European coasts. Given the complete absence of phylogeographic structuring on global and local scales and the inadequate phylogenetic signal of nuclear, mitochondrial, and plastid markers, only general assumptions on the origins of introduced populations and the direction of the spread can be made. Furthermore, significant taxonomic confusion surrounds this species and has been propagated since its first description. This is because no diagnostic morphological characters are known to differentiate between tetrasporophytes (the "*Falkenbergia*" stage, previously described as separate species)

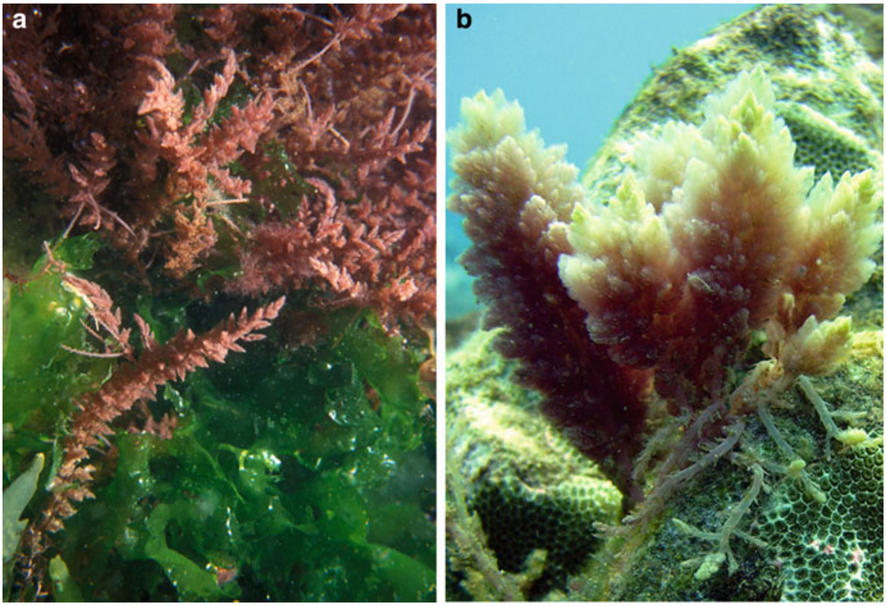

Fig. 12.3 (**a**) *Asparagopsis armata* on *Ulva* (photo by Stefan Kraan; (**b**) unidentified lineage of *Asparagopsis taxiformis* (photo by Mark JA Vermeij)

of *Asparagopsis* species. Although it is easy to identify the macroscopic *A. armata* gametophytes in the field, the identification of cryptic Falkenbergia isolates and their assignment to *A. armata* populations is only feasible with molecular tools or by inference when *Asparagopsis* gametophytes and *Falkenbergia* occur at the same sites.

12.3.5 *Case Study:* Asparagopsis Taxiformis

The warm temperate to tropical red seaweed *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon, 1845, (Fig. 12.3b) consists of four genetically distinct yet morphologically virtually identical mitochondrial lineages, detectable only by molecular tools (the nuclear D1, D2, and D3 hyper-variable domains of the large subunit rDNA gene, the plastid RUBISCO spacer, and the mitochondrial cox2–3 intergenic spacer). One of these, lineage two, is of Indo-Pacific origin and invaded the Mediterranean basin from the Suez Canal (Ní Chualáin et al. 2004; Andreakis et al. 2004, 2007a, b). Phylogeographic patterns inferred from individuals of this species-complex collected globally were suitable to delineate cryptic taxa, infer lineage-specific distribution patterns, and elucidate single or multiple introduction events worldwide. Most importantly, the phylogeographic approach was useful to distinguish between native and invasive cryptic taxa where more than one lineage was found in sympatry. For instance, lineages 1, 2, and 4 co-occur in the Hawaiian archipelago [lineage 2 is considered native and lineage 4 introduced to the islands as recently as in 1991 (Sherwood 2008)]. Lineages 1 and 4 co-occur sympatrically within hundreds of meters in the Pacific side of the Isthmus of Panama and they may represent multiple introduction events. Lineages 2 and 3, the latter of Atlantic distribution, are found in South Africa and are considered introduced and invasive, respectively (Bolton et al. 2011).

Individuals with a *A. taxiformis* morphology collected in unrelated geographic locations have in the past been described as separate species. This observation, together with the multiple ESUs found in *A. taxiformis*, strongly suggests that the taxonomic status of the species sensu stricto needs to be revisited. For instance, one of these lineages may correspond to *A. svedelii* W.R. Taylor (1945), an endemic taxon of the Galápagos Islands, considered synonymous to *A. taxiformis* (Taylor 1945), while cryptic lineage 2 may correspond to *A. sanfordiana* Harvey (Setchell and Gardner 1924), another species considered to be a synonym of *A. taxiformis*.

12.3.6 Case Study: **Codium Fragile** *ssp.* **Tomentosoides**

A single strain of the green alga *Codium fragile* sensu stricto known as *Codium fragile* ssp. *tomentosoides* (Fig. 12.4a) is recognized as highly invasive. DNA sequence analysis based on plastid microsatellites and the plastid *psb*J-*psb*L, *rpl*16-*Rps*3, and *trn*G(UCC)-5 S DNA regions of individuals collected throughout the strain's known native and introduced distribution range indicated extremely low levels of genetic variation with only four distinct haplotypes encountered in Japan where the strain occurs naturally. Despite the limited levels of genetic variability, the phylogenetic signal was sufficient to uncover at least two separate introductions in the biogeographic history of *C. fragile* ssp. *tomentosoides*: two of these haplotypes were highly structured geographically and were found in introduced populations, one exclusively in the Mediterranean Sea, and the other exclusively in Northwest Atlantic, Northern European, and South Pacific populations (Provan et al. 2005, 2008).

12.3.7 Case Study: **Caulerpa** *spp.*

The green algal genus *Caulerpa* comprises morpho-species complexes, species that may become invasive under certain conditions and ESUs known from the literature as "invasive strains" (e.g., described in *C. taxifolia* sensu stricto*)* or "invasive varieties" [e.g., described in *C. racemosa* (Forsskål) J. Agardh sensu stricto (Stam et al. 2006)]. For instance, a potentially invasive species, *Caulerpa prolifera* (Forsskål) J.V. Lamouroux*,* is widely distributed in tropical and subtropical seas and has been significantly altering the structure and functioning in its introduced

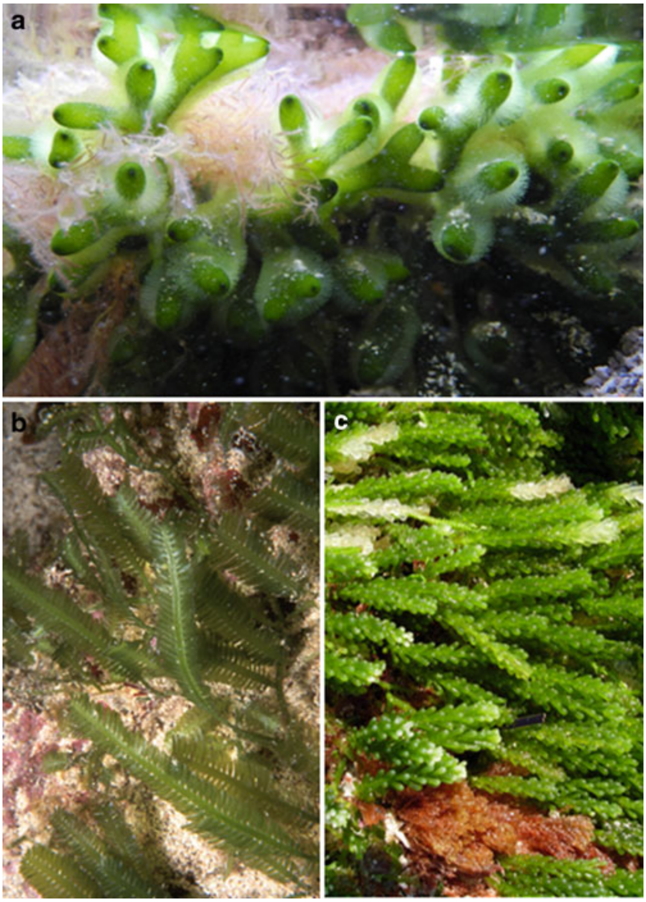

Fig. 12.4 (**a**) *Codium fragile* subsp. tomentosoides (van Goor) P.C.Silva (Algaebase; image Ref. 17373, photo by Mike Guiry); (**b**) *Caulerpa taxifolia* (photo by John Huisman); (**c**) *C. racemosa* var. cylindracea (Sonder) Verlaque, Huisman and Boudouresque (photo by John Huisman)

habitats (e.g., Gab-Alla 2007). The widespread tropical/subtropical seaweed *Caulerpa taxifolia* (Fig. 12.4b), native to the Atlantic, Indian, and Pacific Oceans, was the first seaweed invasion to draw widespread public attention after its introduction to the Mediterranean Sea in the 1980s, its fast spread, and well-documented negative ecological impacts (reviewed in Schaffelke and Hewitt 2007).

Nuclear molecular phylogenies inferred from sequences of the rDNA-ITS1 + 2 region (ribosomal DNA—internal transcribed spacer 1 and 2) from hundreds of *Caulerpa* individuals collected worldwide were used to delineate species, “varieties,” and “strains” of problematic morphological identification. The global phylogenetic reconstruction contributed to the identification of the invasive “aquarium strain” of Australian origin of *C. taxifolia*, which has been introduced at various locations worldwide (Stam et al. 2006). *Caulerpa taxifolia* sensu stricto cannot be distinguished morphologically from this invasive ESU which, following accidental introductions, has successfully established in temperate areas such as the United States, Mediterranean Sea, and southern Australia. Eradication attempts in Australia and the United States (the latter seems to have been successful) and an international ban of this species in the aquarium trade were the initial management responses (Anderson 2007).

The same nuclear marker has been successfully used to uncover the now well-known invasive variety of *Caulerpa racemosa* (*C. racemosa* var. cylindracea (Sonder) Verlaque, Huisman and Boudouresque; Fig. 12.4c) against two other morphologically similar, and apparently noninvasive, sister varieties within the introduced range of the *C. racemosa* complex (*C. racemosa* var. *turbinata–uvifera* (C. Agardh) J. Agardh, *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse f. *requienii* (Montagne) Weber-van Bosse; varieties reviewed by Klein and Verlaque 2008). The approach was particularly useful in the Mediterranean basin where other *C. racemosa* varieties have been erroneously misidentified as the invasive variety (Verlaque et al. 2003, Yeh and Chen 2004; Nuber et al. 2007). Although the invasive lineage represents a dominant algal component in the Mediterranean basin, its identity has been definitely confirmed by combining morphological and molecular data in only five of the 13 Mediterranean countries in which *C. racemosa* sensu stricto has been reported so far (France, Italy, Greece, Croatia, and Cyprus; Klein and Verlaque 2008). This ESU has been introduced into the basin from south-western Australia. Due to its well-documented negative ecological impact, this invasion is considered as one of the most serious biological invasions in the history of species introduced into the basin (Klein and Verlaque 2008).

12.3.8 Assessing Seaweed Introductions

In recent years, several conspicuous seaweed invasions have been detected. Our case studies illustrate that introduced seaweeds may be either genetically homogeneous or species consisting of multiple cryptic lineages.

Populations of taxa in the former category are characterized by weak phylogenetic signals and insufficient phylogeographic structuring between the native and introduced geographical range of the invasive species. Such introduced species are only easy to detect based on morphology if detailed floristic records exist in a particular region. It is however impossible to identify the source populations and the subsequent direction of the invasion based on either morphological identifications or genetic approaches.

Morphologically cryptic species often occur within so-called widely distributed taxa characterized by large geographic disjunctions and apparently low levels of connectivity among populations. The morphological delineation of these ESUs is often impossible even for the expert taxonomist; most importantly, it is difficult to distinguish between a recent introduction and the tendency of the species to disperse naturally (the latter may have occurred in timescales of hundreds to thousands of years before present). However, a molecular phylogeographic approach may represent a sufficiently robust strategy to delineate the cryptic taxa and, most importantly, provide information on the origins of the invader and the direction of the invasion process (see Box 12.1; Voisin et al. 2005; Andreakis et al. 2007a, b; Sherwood 2008).

When cryptic taxa remain unrecognized, significant evolutionary and ecological changes of the local marine biodiversity at the subspecies level will remain unknown. Most importantly, cryptic invasions generally escape the critical management mechanisms of early detection, control, and future prevention. Conversely, if cryptic taxa are misidentified, the impacts of invasions can be erroneously overestimated due to the co-occurrence of morphologically similar invasive and noninvasive cryptic ESUs belonging to the same species-complex.

The increased recognition of cryptic ESUs has significantly changed our view of distribution, abundance, ecophysiology, and conservation status of seaweed species. In the light of the high rate with which new ESUs are discovered, firstly, the taxonomic status of several so-called cosmopolitan species has to be reconsidered. Secondly, the newly emerging patterns can be used to formulate hypotheses on diversification rates and to discover biodiversity hotspots. Thirdly, and most importantly, results are essential to develop accurate assumptions on extinction risks and population sizes. Marine science in the post-genomic period with hundreds of genomes sequenced so far requires a convincing yet suitable taxonomic unit. This is of crucial importance to corroborate ecological, biological, and evolutionary interpretations, but also for practical applications such as management of Marine Protected Areas and active bio-invasion control programs.

12.4 Are Introduced Species a Pest or Prize? A Crab's Tale

The Chinese mitten crab is native to the rivers and estuaries of the Yellow Sea in Korea and China, and has been introduced to many regions of the world. The two quotations below illustrate the *conundrum* whether this crab species is a pest or a prize. Counting the number of scientific publications on this species (ISI web of Knowledge, viewed 05 April 2011) suggests the latter, as most publications report on aspects of economic use, e.g., reproductive performance and breeding optimization.

"*The Chinese mitten crab (*Eriocheir sinensis*) is considered one of the world's top 100 invaders by the Invasive Species Specialist Group (ISSG), part of the Species Survival Commission of The World Conservation Union (IUCN). Populations of* E. sinensis *have recently become established on the west coast of the U.S. and now pose a potential threat to the native fishes and invertebrates and to freshwater and brackish estuarine communities*" (Dittel and Epifanio 2009).

"*The Chinese mitten crab (Eriocheir sinensis) is one of the most important cultivated aquatic species in northern China. Significant advances have been made in the crab farming during last years due to its "high market value with* *declining yields. (…) The annual production of crabs has reached more than 400,000 t valued more than 20 billion RMB in 2005 in China*" (Li et al. 2007).

The food on our tables today comes mostly from a small number of widely cultivated plant and domesticated animal species. Most of them are historical intentional introductions. For example, the earliest archeological records of agriculture in India 2400–1750 BC show crop species of west Asian origin (Hutchinson 1976), while the transport of crop species between Europe, Africa, and Asia peaked with the establishment of direct intercontinental sea trade in the 1400s (National Research Council 1996). There is no evidence that the main crops, such as cereals, oil seeds, fruits, and vegetables, were invasive in their native range. However, over the last 10,000 years modern cultivars (from "*culti*vated *var*iety") have been continuously selected for maximum performance in a range of environments. In addition, modern farming practices such as fertilization, irrigation, crop rotation, the use of pesticides, and genetically assisted breeding have provided extraordinary growth rates and production of high biomass. Interestingly, many invasive seaweed species or ESUs fit the profile of successful agricultural cultivars because they exhibit evolutionary traits for e.g., fast growth, high reproductive capacity, grazing resistance, and wide ecophysiological tolerances to persist in different environments.

12.4.1 Commercially Used Invasive Seaweeds

Seaweeds have been highly valued food resources for thousands of years, especially in Asia. Today, seaweed harvesting and mariculture is an actively growing global industry with a currently estimated total annual value of approximately six billion USD (McHugh 2003). Seaweeds are used mainly as food products for direct human consumption, sources of bulk chemicals such as hydrocolloids and other higher value biochemical compounds, fertilizers, and animal feed additives (see Chap. 22 by Buchholz et al.). The farming of seaweeds has expanded rapidly as demand has outstripped the supply available from natural resources (McHugh 2003).

Many cultivated seaweed species, harvested in their native range, have been intentionally or unintentionally introduced (reviewed in Schaffelke and Hewitt 2007) and are often highly valued for their invasive traits, especially for fast growth rates and biomass accumulation, and often low levels of epiphytism and resistance to herbivores. The commercialization of invasive seaweeds and the exploitation of species-specific invasive traits are often considered to be positive for the economic development of the regional community (Pickering et al. 2007). However, this has to be balanced with the potential negative side effects on the ecological integrity of the "recipient" environments due to accidental release or escape of invasive species, which are difficult to manage. The following sections present brief summaries of the most important commercially used seaweed species, which are also high-profile invaders.

12.4.2 Gracilaria salicornia

Gracilaria species represent well-recognized sources of linear galactan polysaccharide agar, widely used in industry for its excellent gelling or thickening abilities (reviewed in Mehta et al. 2010). Species of the genus *Gracilaria* such as *Gracilaria salicornia* (C. Agardh) Dawson and *G. parvispora* Abbott, a highly valuable alga in the Hawaiian markets, occur widely throughout the tropical Indian and Pacific Oceans (Ryder et al. 2004). Furthermore, *G. debilis* (Forsskål) Børgesen and *G. salicornia* occur naturally at the west coast of India where they represent valuable natural sources for superior quality agars (Oza and Zaidi 2001; Mehta et al. 2010). Several *Gracilaria* species from various sources were intentionally introduced to the Hawaiian Islands for aquaculture development (Russell 1992). *Gracilaria salicornia* has become a successful invader. After escaping from sea farms, *G. salicornia* has invaded surrounding coral reef flats, either as unattached drift or attached populations outcompeting corals, propagated mainly via fragmentation (Smith et al. 2004; Conklin and Smith 2005). *Gracilaria salicornia* displays a variety of biological traits that facilitate high yield cultivation but also make this a potentially invasive species: e.g., high growth rates that can be sustained in variable light regimes, the ability for vegetative dispersal, desiccation tolerance, remarkable tolerance to a wide range of temperatures, salinities, chemical treatments (commercial-grade herbicides and algaecides), and resistance to herbivores (Rodgers and Cox 1999; Smith et al. 2004; Nelson et al. 2009).

12.4.3 Eucheuma *and* Kappaphycus *spp.*

Wild and farmed strains of the carrageenophytes *Eucheuma denticulatum* (Burman) Collins et Harvey, *Kappaphycus alvarezii* (Doty) Doty and *Kappaphycus striatum* (Schmitz) *Doty ex Silva* have been intentionally introduced in more than 20 countries for mariculture purposes (Bulboa and de Paula 2005; Hayashi et al. 2007). These species represent the world's most important kappa-carrageenan producing red algae (Ask and Azanza 2002), a hydrocolloid that is widely used in industry as a gelling and thickening agent. All, however, have been introduced to Kane'ohe Bay in Hawai'i in 1974 for growth experiments and since then accidentally escaped and established highly abundant populations on Hawaii's coral reefs (Conklin and Smith 2005). However, most introductions for cultivation have occurred in the developing world and adverse impacts on the surrounding environment are not well studied (Zemke-White 2004; Bindu and Levine 2011).

Invasive traits that make these species ideal for farming are easy propagation and dispersal by fragmentation and very high growth rate (doubling in size every 15–30 days). The improvement of growth performance in these species is an area of active research (Luhan and Sollesta 2010).

12.4.4 Asparagopsis *Species*

Gametophytes of *Asparagopsis armata* and *A. taxiformis* represent promising sources of pharmaceutical agents of remarkable anti-protozoan, bactericidal, and fungicidal activities (McConnell and Fenical 1977; Woolard et al. 1979; Paul et al. 2006; Salvador et al. 2007; Genovese et al. 2009). In addition, *Asparagopsis* species produce valuable natural secondary metabolites such as compounds with considerable antimicrobial activity against *vibrio harveyi* strains, useful in cosmetics industry and animal aquaculture (Salvador et al. 2007; Manilal et al. 2009); compounds of cytotoxic activity against cancer cells (Zubia et al. 2009) and as preservatives in industrial applications (Kraan and Barrington 2005). Furthermore, "*Falkenbergia*" stages have been successfully cultivated in southern Portugal and can be used as continuous, rapidly growing bio-filter systems for the effluent of commercial fish farms (Schuenhoff et al. 2006; Figueroa et al. 2008; Mata et al. 2010). Introduced in Ireland in 1939, and following population decline due to inadequate temperature for sexual reproduction, *Asparagopsis armata* is now commercially cultivated. The persistence of this species along the Irish West coast seems to be due to continued replenishment from a single aquaculture operation (Kraan and Barrington 2005).

Both *A. taxiformis* and *A. armata* exhibit a number of invasive traits, including vegetative propagation of gametophytes and tetrasporophytes, frequent sexual reproduction of tetrasporophytes, and a suite of halogenated secondary metabolites that increase resistance to herbivory (Boudouresque and Verlaque 2002; Paul et al. 2006; Williams and Smith 2007). In addition, polyploidy has been associated with the extraordinary invasive success of the Indo-Pacific Mediterranean linage 2 of *A. taxiformis* (Andreakis et al. 2009). Furthermore, "*Falkenbergia*" is particularly well suited to human-mediated transport (ballast water) and capable of surviving for long periods as free-floating or loosely attached filaments transported on ships, animals, and other materials in aquaculture (Flagella et al. 2007).

12.4.5 Caulerpa *Species*

Among three genetically distinct ESUs of the *Caulerpa racemosa* species-complex occurring in the Mediterranean Sea, the so-called *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman and Boudouresque, is highly invasive. *Caulerpa* species are greatly valued for human consumption due to their high vitamin and protein content ("sea grapes", *C. racemosa* var *laetevirens*, *C. racemosa*, *C. geminata*, *C. hodgkinsoniae*) or pleasant taste ("green caviar", *C. lentillifera*) and have been identified in several countries as high-value candidates for cultivation and commercial production (Matanjun et al. 2009). *Caulerpa* species also offer promising potential for bioremediation of nutrient-enriched effluent from intensive tropical aquaculture systems because of their high nutrient uptake rates (linked to high growth rates) and the fact that many *Caulerpa* species are native and sufficiently abundant in regions where aquaculture operations are expanding (Paul and de Nys 2008). The downside of the easy cultivation is that several potentially invasive *Caulerpa* species have been commercialized and can be easily purchased from aquarium shops or ordered online. The aquarium industry has enormously facilitated the transportation of these species to distant geographic locations and hence the potential for introductions into natural habitats with serious ecological consequence (Zaleski and Murray 2006; Stam et al. 2006).

The main invasive traits in *Caulerpa* species are high growth rates, propagation via fragmentation (i.e., 1 cm small fragments of *C. taxifolia* are able to give rise to viable single siphonous-cell three-dimensional structures up to 5 m long), broad environmental tolerances, survival out of the water in humid conditions for several days, and in some cases, such as in *Caulerpa racemosa* and *C. taxifolia,* production of secondary metabolites and allelopathic compounds that act as herbivore deterrents and/or inhibit other floral components during space competition (e.g., Meinesz 1999; Vroom and Smith 2001; Gollan and Wright 2006; Wright and Davis 2006; Klein and Verlaque 2008; Raniello et al. 2007).

12.4.6 Ulva *Species*

The cosmopolitan genus *Ulva* Linnaeus, commonly known as the “sea lettuce,” is represented by species distributed in all oceans and estuaries of the world, 17 of which have been recorded in the Mediterranean Sea (Guiry and Guiry 2008). Several species in this genus are commercially cultivated for human consumption in Asian countries or as a component in integrated multi-trophic aquaculture systems, e.g., for bioremediation of effluent and as a feed crop for abalone aquaculture in South Africa (Bolton et al. 2009). Furthermore, due to their higher biomass yield and the higher photosynthetic activity compared to the terrestrial crops, *Ulva* spp. are considered as a promising aquatic crop for biofuel production (Bruhn et al. 2011).

Some Ulva species are problematic to identify morphologically due to the extreme phenotypic plasticity in different environments (Hayden and Waaland 2004). Among them, *Ulva ohnoi* Hiraoka et Shimada, a green-tide-forming alga described from Japan, has been recently found in ballast water tanks of container ships in the Mediterranean Sea and may represent a newly introduced species in the basin (Flagella et al. 2010). *Ulva ohnoi* together with *Ulva prolifera* (Müller) J. Agardh were two of the species responsible for the world largest drifting macroalgal bloom in 2008 estimated as approx. one million tons of harvestable biomass (Qingdao, China, before the Olympic sailing competition; Leliaert et al. 2009; Pang et al. 2010).

Ulva species are well known for their broad environmental tolerance, high growth rate, and photosynthetic activity. They represent early successional, opportunistic species, often occurring in degraded or polluted (high nitrogen) environments, mainly due to their simple morphological features and the high reproductive success supported by the ability of gametes and zoospores to photosynthesize (Beach et al. 1995). Furthermore, *Ulva* species can survive up to 10 months in darkness and are therefore easily transported via ballast water tanks (Santelices et al. 2002).

12.4.7 Undaria pinnatifida

The brown seaweed *Undaria pinnatifida*, commonly known as "wakame," is one of the most commonly eaten seaweeds in Japan. Large-scale commercial cultivation throughout Asia is primarily for human consumption; however, recently discovered antiviral compounds offer prospects for further commercial uses (Hemmingson et al. 2006). Invasive biological traits of *U. pinnatifida* are the very high growth rate (1–2 cm per day), high reproductive rate, long-range dispersal by floating reproductive thalli, the capacity for establishing populations in a variety of habitats and surfaces including artificial substrata, and the ability of gametophytes to colonize ship hulls (e.g., Casas et al. 2004; Thornber et al. 2004; Schaffelke et al. 2005; Russell et al. 2008). Due to the high biomass production and canopy-forming large blades, *U. pinnatifida* often outcompetes other algae by shading and space monopolization; however, ecosystem effects seem to vary greatly between introduced locations (reviewed in Schaffelke and Hewitt 2007).

12.4.8 Codium Fragile *Subspecies* Tomentosoides

Codium fragile (Suringar) Hariot sensu stricto is an edible green alga, widely consumed in Korea, China, and Japan. Cultivated in Korea, using seed stock produced from regeneration of isolated utricles and medullary filaments, the species is preferred to seaweeds such as *Porphyra* and *Undaria* because of its higher market value (Hwang et al. 2008). The protein and amino acid composition in this seaweed is similar to cereals like wheat, corn, and oats; its high content of minerals, dietary fiber, and low lipid content make the species a good candidate as a food additive in human and animal nutrition. In addition, bioactive compounds in *Codium fragile* ssp. *tomentosoides*, including anticancer agents and antibiotics are currently under investigation (Ortiz et al. 2009).

However*, Codium fragile* ssp. *tomentosoides* is one of the most invasive seaweeds, with significant ecological effects ranging from direct competition and replacement of native species to major changes at the community level (reviewed in Schaffelke and Hewitt 2007). In Chile, the invasive *Codium* strain competes with the native agarophyte *Gracilaria chilensis* causing potentially negative effects to the coastal economy by threatening the persistence of *G. chilensis* farms (Neill et al. 2006).

Several biological traits, related to life history and ecology of this ESU, are likely to be a reason for its invasive success. Invasive *Codium* benefits from both sexual and parthenogenetic proliferation as well vegetative propagation facilitated via thalli fragmentation and dispersal. Furthermore, colonization and the persistence of populations are facilitated by broad physiological tolerances to temperature and salinity regimes (Bégin and Scheibling 2003).

12.5 Conclusions

The relocation of marine species with invasive potential represents extraordinary challenges for marine ecosystems. In the future, the rate and range of introductions is likely to increase with increasing volume and speed of maritime traffic and with unprecedented changes in “recipient” environments by global climate change and local habitat degradation. Anticipating and controlling potential invasions is easier and more cost-effective than investing in posteriori management such as control and eradication efforts (e.g., Hewitt et al. 2009b).

The invasive seaweed species discussed in this chapter are recognized priority pest species with a high potential for negative ecological and socio-economic impacts (Doelle et al. 2007). However, where these seaweeds are native, many of them have long been exploited as valuable natural resources. The low capital costs of seaweed farming, good economic returns, and high demand for seaweed products in the world’s market have led to intentional introductions of potentially invasive, high yield taxa like *Kappaphycus*, *Gracilaria*, and *Undaria* spp. and the expansion of farming areas, especially in developing and low-wage countries (Pickering et al. 2007). The incentives to introduce high-yield taxa are significant and the risks of intentional seaweed introductions have not yet been evaluated with cost-benefit analyses that include ecological and socio-economic consequences. The seaweed industry in the new millennium is predicted to grow with increasing demand for traditional seaweed products and for new applications of seaweeds, e.g., for the production of biofuels and bioactive compounds. Selective breeding and genetic modification to produce better cultivars for these applications is likely to add another dimension of uncertainty. New “super strains” with high invasive potential may be introduced to new locations with unprecedented consequences or may interbreed with con-specific native populations and increase their invasiveness.

The potential for controlled harvest has been suggested as a positive consequence of seaweed introductions, especially in areas where invasive seaweeds have established in high abundance and eradication or ongoing control is not economically feasible. However, stringent harvest regulations must be developed and applied to prevent further translocation and spread of invasive seaweeds into areas previously unaffected (see Schaffelke and Hewitt 2007).

In application of the precautionary principle of environmental management, preference should be given to the development of sustainable commercial seaweed culture in regions where a species (sensu stricto) occurs naturally. Valuable marine cultivars could be certified similar to D.O.P (protected denomination of origin) and D.O.C (controlled origin denomination) standards of agricultural crops, which would confirm that a seaweed has been produced in a specific geographical location. In addition, marine stewardship certifications would attest that a product is produced under certain environmental management and product quality standards. However, for this to happen seaweed products must attain a much higher commercial value than they currently have. In the meantime, a number of international agreements and voluntary codes of practice have been formulated to encourage national governments to restrict and control the intentional import and use of NIMS in aquaculture (reviewed in Hewitt et al. 2006). Also, recommendations for the assessment of proposals for intentional introductions are available to assist industries and regulators, even though quantitative data on ecological and socio-economic impacts of seaweed introductions are scarce. Research describing and assessing past and present NIMS invasions is vital to better predict future invaders, invaded regions, and the associated impacts and to support management and conservation decisions. At present, many questions around seaweed invasions and marine invasions, in general, remain to be answered (see e.g., Johnson 2007).

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