

Adaptation mechanisms and ecological consequences of seaweed invasions: a review case of agarophyte *Gracilaria vermiculophylla*

Zi-Min Hu · Lopez-Bautista Juan

Received: 12 February 2013 / Accepted: 18 September 2013 / Published online: 26 September 2013
© Springer Science+Business Media Dordrecht 2013

Abstract To prioritize management, conservation and restoration from seaweed invasions, it is important for policy-makers to elucidate the ecological mechanisms during the three phases of invasion: introduction, establishment, and diffusion. In this review, we synthesize the current knowledge of the invasion mechanisms and ecological impacts of *Gracilaria vermiculophylla*, a red agarophyte native to Asia Northwest Pacific, which now has become a rapid and successful coastal invader in the Atlantic and Eastern Pacific Oceans. Eco-physiological and chemical studies have revealed that some ecological traits, including survival in dark condition (e.g. the ballast water), tolerance to grazing and extreme salinities and temperatures, insensitive to UVR and light intensity and nutrient levels, adaptation to a wide diversity of habitats, and chemical defense to potential predators, may provide *G. vermiculophylla* an unmatched advantage during its global invasion. The rapid growth, flexible reproduction through fragmentation, efficient recruitment on hard substratum, seeding success on various vectors, and interaction with local community organisms may also contribute to its rapid increase in

abundance and effects on the invaded coastal ecosystems. *G. vermiculophylla* showed both negative and positive impacts to the marine ecosystems through changing interspecific competition, increasing habitat diversity, altering the community complex, and transforming biogeochemical cycles and estuarine food webs. Future surveys such as marine exotic genomics, transcriptome sequencing and epigenetic variation between native and invasive entities may provide insightful promise on molecular mechanisms of seaweed invasion.

Keywords Ecological consequences · *Gracilaria vermiculophylla* · Habitat modifier · Invasion mechanisms · Seaweed

Introduction

The coastal ecosystem is among the most significant components on earth in the ecological and socio-economic context, approximately providing over US\$14 trillion worth of ecosystem goods and service (c. 43 % of the global total) each year (Costanza et al. 1997; Harley et al. 2006). However, this system is now facing severe threats from increasing invasive marine organisms. It is notable that seaweed invasions have been demonstrated to generate drastic negative impacts on coastal community structure, species abundance and

Z.-M. Hu (✉)
Institute of Oceanology, Chinese Academy of Sciences,
Qingdao 266071, China
e-mail: huzimin9712@163.com

Z.-M. Hu · L.-B. Juan
Department of Biological Sciences, The University of
Alabama, Tuscaloosa, AL 35487, USA

richness, and fundamental processes (Inderjit et al. 2006; Williams and Smith 2007). Such a situation demands a better understanding of the adaptive mechanisms of representative invasive seaweeds in a new system, in order to develop science-oriented theory and strategy for future management, restoration and conservation (Schaffelke et al. 2006; Hewitt et al. 2007).

Gracilaria vermiculophylla (Ohmi) Papenfuss is an agar producing red seaweed endemic in the Asia-Northwest Pacific region (Ohmi 1956; Yoshida et al. 1995). During the past three to four decades, this seaweed has successfully invaded many coastal habitats around the globe, with introductions in the eastern Pacific (Baja California, Mexico and British Columbia, Canada) (Bellorin et al. 2004; Saunders 2009), the mid-western Atlantic (Virginia, North Carolina and New England) (Thomsen et al. 2005; Freshwater et al. 2006; Nettleton et al. 2013), and the eastern Atlantic including France, Spain, Portugal, the Mediterranean Sea, Germany, Netherlands, Sweden and the Baltic Sea (Barbara et al. 2005; Rueness 2005; Thomsen et al. 2007; Weinberger et al. 2008; Guillemin et al. 2008; Sfriso et al. 2010). After invading a new system, *G. vermiculophylla* either establishes as abundant unialgal entangled mats in estuaries, or form expansive blooms in coastal lagoons (Thomsen et al. 2007; Pinon-Gimate et al. 2008; Abreu et al. 2011a), producing significant impacts on coastal ecosystems and environments. For example, in Hog Island Bay, Virginia, the invaded *G. vermiculophylla* became the dominant seaweed and made up 74 % of the total biomass across all study sites during 1998 and 2002 (Thomsen et al. 2006). As a consequence, unveiling the potential ecological and physiological mechanisms responsible for its rapid global invasion has stimulated much interest in the phycological community (Rueness 2005; Weinberger et al. 2008; Thomsen 2010; Abreu et al. 2011b; Nylund et al. 2011; Nejrup and Pedersen 2012; Rempt et al. 2012; Roleda et al. 2012; Nettleton et al. 2013).

Numerous empirical studies revealed that various ecological traits, including a versatile reproductive system, allowed *G. vermiculophylla* to succeed in different invaded environments and produced both negative and positive impacts on the new ecosystems. More specifically, *G. vermiculophylla* has been placed among the four most potential invaders out of 114 non-indigenous macroalgal species in Europe (Nyberg 2007), according to the proposed 13 traits for estimation

of potential macroalgal dispersal, settlement and ecological effect (Nyberg and Wallentinus 2005). In this review, we catalogued multiple biotic and abiotic traits contributing to global invasion of *G. vermiculophylla* and relevant ecological consequences. We also highlight future research that needs to decipher the molecular mechanisms for seaweed invasions.

Adaptation mechanisms: transoceanic migration

The reproductive versatility in a life-cycle may be a significant biotic trait facilitating inter-regional introduction for the seaweeds. An experimental survey has revealed that the unique capacity of vegetative propagation is fundamental to the successful colonization of some non-indigenous seaweeds (Nyberg and Wallentinus 2005). *G. vermiculophylla* is a perennial macroalga with an isomorphic life cycle (Abreu et al. 2011a). It can reproduce sexually and asexually (vegetative fragmentation), showing a rapid growth from germling (a visible cystocarp formation after 18 days and carpospores release after 35 days) to sexual maturity (dioecious gametophyte mature after three to four months) (Rueness 2005; Abreu et al. 2011a). In natural habitats, *G. vermiculophylla* can easily reproduce by means of sporic and vegetative fragmentation (Nettleton et al. 2013), even a size as small as 1 mm can survive and continue to grow after detachment (Abreu et al. 2011a). Laboratory studies also found that this unique trait can enable *G. vermiculophylla* thrive on bivalve shells and man-made structures during a long-distance transportation (Rueness 2005; Thomsen and McGlathery 2007; Nyberg and Wallentinus 2009). Even in the newly invaded area, the fragmented *G. vermiculophylla* can grow in lagoons and estuarine environments by either loose-lying or attaching, increasing the probability of successful establishment and spread (Sakai et al. 2001).

As with many other successful invaders, the invasion of *G. vermiculophylla*, mediated by human activities, involves some vital traits for its survival during the transportation, such as the ability to tolerate darkness, extreme temperatures and starvation, and even to dehydrate. Nyberg and Wallentinus (2009) found that *G. vermiculophylla* from the west coast of Sweden could survive more than five months at 8 °C under total darkness, even with a dehydration of up to

19 %. Hence, this seaweed is well adapted to transport in ballast water or on ship decks. In particular, the re-growth of new shoots was observed when the thallus was re-exposed to photosynthetically active radiation (PAR) ($265 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$). These findings suggest that even small fragments carried in fishing nets, ballast tanks, diving equipment, or by migrating seabirds may lead to the introduction of *G. vermiculophylla* into new areas (Nyberg and Wallentinus 2009).

Adaptation mechanisms: establishment and expansion in new coastal systems

The steady establishment in the invaded region is a crucial phase for population growth and range expansion of invasive marine organisms. *G. vermiculophylla* is among the most notorious invasive seaweeds known to date in North America and Europe with large abundance and high dispersal rate (Nettleton et al. 2013). It extended its distribution range in Sweden by ca. 150 km from 2003 to 2005 (Nyberg et al. 2009), similar to another red alga *Heterosiphonia japonica* which recently was found to invade the western North Atlantic coastline with a range of more than 700 km between 2007 and 2012 (Newton et al. 2013a). More recently, with the integration of herbarium collections, Nettleton et al. (2013) reported that *G. vermiculophylla* invaded a wide range (over 500 km) in New England, USA probably since 2000, such an expansion rate is comparable to other various invasive brown macroalgae, *Undaria pinnatifida* (Harvey) Suringar in Southern England (44 km per year) and *Sargassum muticum* (Yendo) Fensholt in Denmark (15–17 km per year) (Staehr et al. 2000; Farrell and Fletcher 2006). Nevertheless, all these seaweed invasions showed a general pattern: an initial fast expansion typically followed by a severe slow-down or even decline, which may partly due to incomplete field survey or habitat unsuitability of adjoining ecosystems.

Recent studies revealed that the success invasion of *G. vermiculophylla* across a wide range of coastal environments might result from some important ecological and physiological processes, including high recruitment, high tolerance to sedimentation,

desiccation, grazers, light, and salinity extremes. These potential biotic and abiotic mechanisms are briefly listed as follows:

1. Photosynthesis and growth of *G. vermiculophylla* can be significantly affected by levels of salinity. Although the optimal salinities for its growth are from 15 to 30 ppm (Rueness 2005; Kim et al. 2012), the euryhaline *G. vermiculophylla* can live and grow slowly at extreme salinity as low as 0.5 ppm in spring and autumn (Weinberger et al. 2008). It has been reported that the thalli are still able to survive 8 weeks under salinity of 60 ppm (Yokoya et al. 1999).
2. *G. vermiculophylla* is eurythermal as well, and it can reach the higher optimum growth at temperature between 11 and 30 °C (Yokoya et al. 1999; Rueness 2005; Abreu et al. 2011a). Likewise, the thalli can still survive with the minimal growth at temperature extremes such as 2 and 35 °C (Yokoya et al. 1999; Raikar et al. 2001). Apparently, this euryhaline and eurythermic trait enables *G. vermiculophylla* the ability to tolerate a wide range of marine habitats.
3. As mentioned previously, ultraviolet radiation (UVR, 280–400 nm) is one of the important stress factors that could influence the fitness and survival of both native and alien seaweed species (Häder et al. 2011). *G. vermiculophylla* has multiple UVR defense mechanisms to cope with changing light quantity and quality found in the new habitat. Such photoprotective mechanisms may contribute its resistance to the desiccation with high solar radiation (Roleda et al. 2012), allowing *G. vermiculophylla* to live in habitats where the UVR fluctuates, such as intertidal mudflats, lagoons, estuaries, and even aquaculture facilities.
4. Photosynthetically, this seaweed is well adapted to low light conditions, which endow *G. vermiculophylla* a competitive advantage over local macroalgae in invaded coasts (Jensen et al. 2007). For instance, although the Danish estuaries are historically highly eutrophic (Kronvang et al. 1993), leading to a decrease in primary production for benthic flora via increased shading in the water column (Meyercordt et al. 1999). *G. vermiculophylla* has rapidly invaded some Danish estuaries such as Holckenhavn Fjord, northern Funen and

the inlet of Limfjorden (Thomsen et al. 2007) since it was first discovered in 2003. As such, in the SW Baltic Sea, the growth of *G. vermiculophylla* is only restricted above a depth of three meters during the summer (Weinberger et al. 2008).

5. Grazing preference and performance of native predator on invasive seaweed is another fundamental force driving successful invasion (Teso et al. 2009). However, recent studies demonstrated that *G. vermiculophylla* is able to tolerate grazing. In Denmark, Jensen et al. (2007) found two local invertebrate grazers (*Idotea baltica* and *Littorina littorea*) clearly preferring the green alga *Ulva lactuca* when it is available with other two algal species (*Fucus vesiculosus* and *G. vermiculophylla*). Even when only *F. vesiculosus* and *G. vermiculophylla* are present, both grazers especially prefer the former to the latter in the western Baltic Sea (Weinberger et al. 2008; Jensen et al. 2007). This suggests a potential defense mechanism against generalist herbivores. The latest comparative feeding tests in FynsHoved, Denmark, showed that the native invertebrate grazers only consume *G. vermiculophylla* in no-choice trials, and generally avoided this alga when there is another food source available (Nejrup and Pedersen 2012).

In terms of ecological interactions, such an observation is subsequently confirmed by intense herbivore feeding trails and stimulated experiments. Nylund et al. (2011) assessed the mechanistic defenses of invasive *G. vermiculophylla* from the Baltic Sea using mass spectrometry based on metabolomics in combination with bioassays. Their results suggest that *G. vermiculophylla* chemically deters herbivores by two lines of defense, a rapid wound-activated process followed by a slower inducible defense. Coincidentally, a more recent study revealed that the invasive *G. vermiculophylla* cultured in laboratory exhibited a unique wound-activated chemical defense, which was manipulated by the structurally diverse oxylipins, making it active against the herbivorous predator sea snail (*Echinolittorina peruviana*) (Rempt et al. 2012). This chemical defense mechanism may facilitate the long-term maintenance of invaded *G. vermiculophylla* populations and rapid expansion into adjacent areas.

6. Besides the intertidal environments such as salt marshes, fine sand, mudflats, stones and small

rocks, *G. vermiculophylla* is also well adapted to habitats with high-sedimentation. Thomsen and McGlathery (2007) reported that *G. vermiculophylla* decomposed more slowly than two green algae *Ulva curvata* (native) and *Codium fragile* (introduced) in Hog Island Bay, Virginia. Particularly, its tissue appeared structurally intact and healthy even after a week of complete burial.

7. Like other factors (e.g. light, space), nutrient is another essential element affecting the survival, growth and reproduction of seaweeds (Lobban and Harrison 1997). However, *G. vermiculophylla* was not negatively affected by either high or low light intensity or nutrient levels (Thomsen and McGlathery 2007; Abreu et al. 2011a). In other words, the ability of *G. vermiculophylla* to utilize various levels of concentration of nitrogen and light allow it for a competitive advantage over other native algal species (Jensen et al. 2007).
8. The fronds of *G. vermiculophylla* can be prone to fragmentation by physical disturbances like tide currents and predators, and persist as both small and large vegetative fragments (Thomsen and McGlathery 2005). Afterwards, the drifting fragments of *G. vermiculophylla* can accumulate in shallow and sheltered waters and form perennial mats, which can be dispersed by oceanic currents in wide coastal ranges (Weinberger et al. 2008). In addition, *G. vermiculophylla* thalli can even attach to the tube-building polychaete (*Diopatra cuprea*). Studies showed that such an attachment behavior might facilitate its invasion in some Northwest Atlantic habitats (Thomsen et al. 2005; Berke 2012).

Ecological consequences: effects on local species

Several studies have revealed that invading seaweeds have caused some demographic consequences to native species through competitive interactions. To quantify the direction and magnitude of impacts on native species, a recent meta-analysis of 18 manipulated experiments implemented by Thomsen et al. (2009a) showed that the invasion of non-indigenous seaweeds have, on average, small-to-large negative impacts on native macrophyte abundance and assemblages over temporal and spatial scales. As exemplified in another field study, Thomsen et al. (2009b)

reported that there is significantly different biota associated with *G. vermiculophylla* in lagoon and salt marsh habitats in Virginia, USA, particularly lower species richness and biomass. The associated biota can be cataloged in three assemblages: (1) the marine stenohaline and desiccation-intolerant organisms mostly found on lagoon *G. vermiculophylla*, such as *Ceramium* spp. and *Polysiphonia* spp., amphipoda *Caprella* spp., crab *Pagarus* spp., and many amphipods; (2) some stress-tolerant euryhaline organisms colonizing *G. vermiculophylla* can also survive in lower marshes, including *Ulva* spp., sea snail *Astyrislunata* and several polychaetes; and (3) some organisms mainly colonize *G. vermiculophylla* in marsh such as *Bostrychia* spp., snail *Hydrobia* spp. and *Ilyanassa obsoleta*, crab *Sesarma* sp. and *Uca* sp. (Adam 1990). Notably, *Hydrobia* and *Ilyanassa* in the latter assemblage can also be found on intertidal mudflats but are not obligate marsh organisms (Lippson and Lippson 1997), suggesting an alga-mediated transfer of organisms from lagoon to marsh habitats (Thomsen et al. 2009b).

In the Baltic Sea, the drifting or attached populations of *G. vermiculophylla* can also cover the hard sediments, interfere with the main native perennial alga *F. vesiculosus*, and even overgrow and shade its flourish (Weinberger et al. 2008). In the embayments and estuaries of New England and Long Island Sound, USA, the invasive *G. vermiculophylla* has become the dominant seaweed species and has replaced the native species *G. tikvahiae* (Nettleton et al. 2013). Experimental results showed that *G. tikvahiae* stopped growth or even exhibited negative growth rates at sub-optimal environmental conditions (<20 psu and <20 °C), whereas the invasive *G. vermiculophylla* grew equally well at temperature as low as 5 °C and in the salinity range of 15–30 psu (Kim et al. 2012). Such ecophysiological responses indicates that the tolerance to hypo-osmotic environmental stresses enables *G. vermiculophylla* to have an overwhelming competitive advantage to native congeneric species, and thus facilitate its establishment and rapid spread in new habitats.

Ecological consequences: interaction with the new community system

The influence between the invasive species and native organisms can also be interactive. The latest

quantitative surveys along Georgia and South Carolina coast, USA, have revealed that the density of the native onuphid polychaete *Diopatra cuprea* and the above ground height of its biogenic tubes can produce positive impact on the biomass of *G. vermiculophylla*. In return, the increasing biomass of *G. vermiculophylla* facilitated the abundance of associated epifauna, which are composed primarily of amphipods and small snails (Byers et al. 2012). In Ria De Aveiro, Portugal, Cacabelos et al. (2012) discovered that the shift from monospecific native eelgrass *Nanozostera noltii* to assemblages dominated by invaded *G. vermiculophylla* in coastal ecosystem can lead to a lower community efficiency (i.e. productivity per unit of biomass). But the same replacement scenario can produce higher assemblage productivity (e.g. productivity per square meter) in *G. vermiculophylla* beds.

Ecological consequences: negative impacts on the community system

As previously reported in some marine invaders (Lambert et al. 1992; Crooks and Khim 1999), invasive seaweed not only generate impacts on macrophytes or invertebrates, but also on the entire coastal community. We can extrapolate that the floating seaweed mats formed by *G. vermiculophylla* may serve as physical barriers for settling larvae unable to find the sediment below the algal canopy, because similar effects have been observed in floating green macroalgal mats (Bonsdorff 1992; Auffrey et al. 2004). After the establishment, the flourishing growth of *G. vermiculophylla* can decrease the light intensities and change water movements, which subsequently affects the local species directly in and on the sediment and thus the food availability for deposit feeders (Madsen et al. 2001; Nyberg et al. 2009).

As mentioned above, invaded *G. vermiculophylla* has produced negative effects on the abundance and distribution of eelgrass, which provide key ecological services in tropical and temperate ecosystem, including organic carbon production and export, nutrient cycling, sediment stabilization, enhanced biodiversity, and trophic transfers to adjacent habitats (Orth et al. 2006). Field surveys found that dense mats formed by invasive *G. vermiculophylla* can shade eelgrass (*Zostera*) beds, inhibit its growth and change the function of coastal ecosystem. In some cases, *G. vermiculophylla*

often grows in the same locations as the dwarf eelgrass *Z. noltii* and *Z. marina*, and induces harmful effects on their metabolism and survival with synergistic effects of temperature (Martínez-Lüscher and Holmer 2010), suggesting possible greater impact of this invasive species under future higher water temperatures. Recent experimental surveys showed that the invasion of *G. vermiculophylla* could lead to the acceleration of habitat loss for native *F. vesiculosus* after one more year in the Baltic Sea because of their overlapped distributional ranges (Weinberger et al. 2008). In Kiel Fjord the extended *G. vermiculophylla* mats often cause oxygen deficiency due to the excessive input of decomposing organic matter, resulting in changes of diversity and composition of sheltered infauna (Weinberger et al. 2008). Similar patterns were found by another red alga *Heterosiphonia japonica*, native to the western North Pacific, which has rapidly invaded the western North Atlantic coasts since 2007. It is reported that this alga comprised of up to 60–80 % of the biomass in subtidal community structure, leading to significant lower species richness in the recipient systems (Newton et al. 2013a).

Economically, seaweed invasions also have been responsible for the collapse of local fisheries, tourism, aquaculture and marine infrastructure. It is reported that after invading the Cape Fear River estuary, North Carolina, USA, *G. vermiculophylla* acts as a nuisance for fishing industries and even hampers the commercial fishing operations (Freshwater et al. 2006). However, the potential commercial effect needs to be carefully evaluated.

Ecological consequences: positive impacts via creating habitat complexity and enhancing local diversity

Although invasive populations of *G. vermiculophylla* have shown adverse impacts on the coastal ecosystems, it may benefit shelter-dependent species by altering the complexity of un-vegetated habitats such as mud and sand flats. Thomsen et al. (2006) found that *G. vermiculophylla* enhanced the local diversity of some taxa like *Polysiphonia*, *Ceramium*, *Bryopsis*, *Ectocarpus* and *Champia* in Hog Island Bay, Virginia, by adding hard-substratum availability for attachment and entanglement of other algal species. In low energy shallow embayments, estuaries, lagoons and harbors,

the loose-lying *G. vermiculophylla* can potentially develop into dense floating mats, which can function as modified habitat for benthic faunal community and bottom dwelling organisms, including *Hydrobia ulvae* and *L. littorea*, and even juvenile crabs (Nyberg et al. 2009; Abreu et al. 2011b).

Nyberg et al. (2009) found that the animal abundances were positively correlated with the biomass of algae and plants associated with *G. vermiculophylla* in Virginia, USA and Sweden. Particularly, the invasion of *G. vermiculophylla* in non-vegetated soft-sediment estuaries may benefit the abundance of small native invertebrates (e.g. gastropods and crustaceans) and epiphytic algae. In 2010, Thomsen (2010) also reported that the invasive *G. vermiculophylla*, either at low or high densities, can create more diverse and suitable habitats for most macro-invertebrates (>2 mm) inhabiting *Zoster marina* eelgrass beds at Snaptun Harbor, Denmark. Similarly, Johnston and Lipcius (2012) reported that *G. vermiculophylla* could form a nursery habitat for the native blue crab (*Callinectes sapidus*) in Chesapeake Bay, Virginia, thereby compensating for severe declines in eelgrass. A more recent survey (Newton et al. 2013b) highlighted that *G. vermiculophylla* may provide a novel hard substrate for egg capsule deposition of a native intertidal mud snail (*Ilyanassa obsoleta*), with the abundances of eggs on *G. vermiculophylla* 11–50 times greater than those on other co-occurring native macrophytes. Interestingly, the thick layer of egg capsules on *G. vermiculophylla* did not produce detrimental influences on its growth, whereas the growth of a native red alga (*Ceramium virgatum*) was drastically reduced when egg capsules are present (Newton et al. 2013b).

Ecological consequences: positive impacts via changing biogeochemical cycles

Seaweed invasions may transform marine coastal ecosystems by adding excessive amount of resources (notably nitrogen), and potentially alter the flow, availability, or quality of nutrient resources in biogeochemical cycles. Field studies showed that *G. vermiculophylla* makes up 85–90 % of the biomass in Hog Island Bay, Virginia and can take advantage of pulsed urea availability in coastal waters and serve as a potential nitrogen source for primary producers (Tyler et al. 2005; Tyler and McGlathery 2006). In shallow

coastal ecosystems, the invasive *G. vermiculophylla* can also increase sediment suspension and enhance the nutrient flux from the sediment to the water column at low densities of biomass (Lawson et al. 2012).

Ecological consequences: positive impacts via changing estuarine food webs

Both field surveys and manipulative experiments showed that in the novel systems *G. vermiculophylla* favor intertidal and shallow subtidal photic zones by anchoring, while the native worm *Diopatra* can facilitate high levels of net primary productivity (up to 1 kg/m²; mean = 40 g/m²) (Byers et al. 2012). This ecological scenario suggests that *G. vermiculophylla* represents an enormous, novel source of primary production in a mudflat habitat previously devoid of algal biomass, and has created profound effects on cycling of materials within estuarine detrital food webs under proper conditions (Byers et al. 2012).

Perspectives

Seaweed invasions have become one of the growing global concerns through producing multiple levels of ecological consequences on local tidal communities and marine ecosystems. The numerous eco-physiological studies on *G. vermiculophylla* provide an insight platform to fully understand what kind of potential mechanisms contribute to its transoceanic migration, establishment and global expansion (Rueness 2005; Thomsen et al. 2006; Thomsen and McGlathery 2007; Nyberg et al. 2009; Abreu et al. 2011a; Nettleton et al. 2013). However, these large-scale laboratory and field surveys are either sparse or lack standardized approaches, leading to some results that cannot be assessed or integrated. Hence, building a global international network with standardized protocol designs and implementations (e.g. the creation of opened database and the share of ideas and data), would be a significant step toward ultimate ecological detection, biosecurity assessment, and scientific management of invasive seaweeds.

Genetic diversity and time are crucial and necessary factors for evolutionary adaptation. However, some invasive seaweeds are characterized with elevated high genetic homogeneity, indicating that potential

compensatory mechanisms may exist to allow for short-term adaptation to the invaded systems (Pérez et al. 2006). Interestingly, because frequent exposure to novel ecological niches has been shown to affect the genome stability of seaweed species (Henikoff 2005; Bond and Finnegan 2007), the new advances in biotechnology, including adaptation genomics and epigenetic variation, may potentially yield genome-scale insights on succession of invasive seaweeds to novel environments (Schrey et al. 2012). More importantly, some previous surveys have revealed that stress-induced genome modifications can be stably inherited when retrotransposons are activated and reinserted into the genome (Cullis 2005; Bond and Finnegan 2007). The decrease in genome stability can cause modifications to the transcriptome scale in response to environmental stimuli (Prentis et al. 2008), which has recently been demonstrated in the globally invasive fireweed (*Senecio madagascariensis*) (Prentis et al. 2010) and the cordgrass sister species (*Spartina maritima* and *S. alterniflora*) (Chelaifa et al. 2010; De Carvalho et al. 2013). In summary, we can expect that exotic genomics, epigenetic process and transcriptome sequencing, can potentially make a significant contribution to better understand the molecular mechanisms on seaweed invasions in the coming years.

Acknowledgments We thank everyone who shared with us observations from both experimental and field surveys. We are grateful to two anonymous reviewers for their valuable and constructive comments on the original version of the manuscript. This work was supported by National Natural Science Foundation of China (No. 31000103) granted to Z. M. Hu, and by the US National Science Foundation Assembling the Tree of Life Program (DEB-1036495, DEB-0937978) granted to JMLB.

References

- Abreu MH, Pereira R, Sousa-Pinto I, Yarish C (2011a) Nitrogen uptake response of *Gracilaria vermiculophylla* (Ohmi) Papenfuss under combined and single addition of nitrate and ammonium. *J Exp Mar Biol Ecol* 407:190–199
- Abreu MH, Pereira R, Sousa-Pinto I, Yarish C (2011b) Ecophysiological studies of the non-indigenous species *Gracilaria vermiculophylla* (Rhodophyta) and its abundance patterns in Ria de Aveiro lagoon, Portugal. *Eur J Phycol* 46:453–464
- Adam P (1990) Salt marsh ecology. Cambridge University Press, Cambridge
- Auffrey LM, Robinson SMC, Barbeau MA (2004) Effect of green macroalgal mats on burial depth of soft-shelled clams *Mya arenaria*. *Mar Ecol Prog Ser* 278:193–203

- Barbara I, Cremades J, Calvo S, Lopez-Rodriguez MC, Dosil J (2005) Check-list of the benthic marine and brackish Galician algae (NW Spain). *An Jard Bot Madr* 62:69–100
- Bellorin AM, Oliveira MC, Oliveira EC (2004) *Gracilaria vermiculophylla*: a western Pacific species of Gracilariaceae (Rhodophyta) first recorded from the eastern Pacific. *Phycol Res* 52:69–79
- Berke SK (2012) Biogeographic variability in ecosystem engineering: patterns in the abundance and behavior of the tube-building polychaete *Diopatra cuprea*. *Mar Ecol Prog Ser* 447:1–13
- Bond DM, Finnegan EJ (2007) Passing the message on: inheritance of epigenetic traits. *Trend Plant Sci* 12:211–216
- Bonsdorff E (1992) Drifting algae and zoobenthos—effects on settling and community structure. *Neth J Sea Res* 30:57–62
- Byers JE, Gribben PE, Yeager C, Sotka EE (2012) Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. *Biol Invasions* 14:2587–2600
- Cacabelos E, Engelen AH, Mejia A, Arenas F (2012) Comparison of the assemblage functioning of estuary systems dominated by the seagrass *Nanozostera noltii* versus the invasive drift seaweed *Gracilaria vermiculophylla*. *J Sea Res* 72:99–105
- Chelaifa H, Mahe F, Ainouche M (2010) Transcriptome divergence between the hexaploid salt-marsh sister species *Spartina maritima* and *Spartina alterniflora* (Poaceae). *Mol Ecol* 19:2050–2063
- Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260
- Crooks JA, Khim HS (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *J Exp Mar Biol Ecol* 240:53–75
- Cullis CA (2005) Mechanisms and control of rapid genomic changes in flax. *Ann Bot (London)* 95:201–206
- De Carvalho JF, Poulain J, Silva CD, Wincker P, Michon-Coudouel S, Dheilly A, Naquin D, Boutte J, Salmon A, Ainouche M (2013) Transcriptome de novo assembly from next-generation sequencing and comparative analyses in the hexaploid salt marsh species *Spartina maritima* and *Spartina alterniflora* (Poaceae). *Heredity* 110:181–193
- Farrell P, Fletcher RL (2006) An investigation of dispersal of the introduced brown alga *Undaria pinnatifida* (Harvey) Suringar and its competition with some species on the man-made structures of Torquay Marina (Devon, UK). *J Exp Mar Biol Ecol* 334:236–243
- Freshwater DW, Montgomery F, Greene JK, Hamner RM, Williams M, Whitfield PE (2006) Distribution and identification of an invasive *Gracilaria* species that is hampering commercial fishing operations in southeastern North Carolina, USA. *Biol Invasions* 8:631–637
- Guillemin ML, AitAkki S, Givernaud T, Mouradi A, Valeo M, Destombe C (2008) Molecular characterization and development of rapid molecular methods to identify species of Gracilariaceae from the Atlantic coast of Morocco. *Aquat Bot* 89:324–330
- Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL (2006) The impacts of climate change in coastal marine systems. *Ecol Lett* 9:228–241
- Henikoff S (2005) Rapid changes in plant genomes. *Plant Cell* 17:2852–2855
- Hewitt CL, Campbell ML, Schaffelke B (2007) Introduction of seaweeds: accidental transfer pathways and mechanisms. *Bot Mar* 50:326–337
- Inderjit Chapman D, Ranalletti M, Kaushik S (2006) Invasive marine algae: an ecological perspective. *Bot Rev* 72:153–178
- Jensen AT, Uldahl AG, Sjogren KP, Khan M (2007) The invasive macroalgae *Gracilaria vermiculophylla*—effects of salinity, nitrogen availability, irradiance and grazing on the growth rate. Master thesis, Department of Environmental, Social and Spatial Change, Roskilde University, Denmark
- Johnston CA, Lipcius RN (2012) Exotic macroalga *Gracilaria vermiculophylla* provides superior nursery habitat for native blue crab in Chesapeake Bay. *Mar Ecol Prog Ser* 467:137–146
- Kim JK, Kovtun K, Yarish C (2012) Tolerance to hypo-osmotic stress and low temperature determines the spread of non-indigenous *Gracilaria vermiculophylla*. *J Phycol* 48:S46
- Kronvang B, Aertebjerg G, Grant R, Kristensen P, Hovmand M, Kirkegaard J (1993) Nationwide monitoring of nutrients and their ecological effects—state of the Danish aquatic environment. *Ambio* 22(4):176–187
- Lambert WJ, Levin PS, Berman J (1992) Changes in the structure of a New England (USA) kelp bed: the effects of an introduced species? *Mar Ecol Prog Ser* 88:303–307
- Lawson SE, McGlathery KJ, Wiberg PL (2012) Enhancement of sediment suspension and nutrient flux by benthic macrophytes at low biomass. *Mar Ecol Prog Ser* 448:259–270
- Lippson AJ, Lippson RL (1997) Life in the Chesapeake Bay. The John Hopkins University Press, Baltimore
- Lobban CS, Harrison PJ (1997) Seaweed ecology and physiology. Cambridge University Press, Cambridge
- Madsen JD, Chambers PA, James WF, Koch EW, Westlake DF (2001) The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* 444:71–84
- Martinez-Lüscher J, Holmer M (2010) Potential effects of the invasive species *Gracilaria vermiculophylla* on *Zostera marina* metabolism and survival. *Mar Environ Res* 69:345–349
- Meyercordt J, Gerbersdorf S, Meyer-Reil LA (1999) Significance of pelagic and benthic primary production in two shallow coastal lagoons of different degrees of eutrophication in the southern Baltic Sea. *Aquat Microb Ecol* 20(3):273–284
- Nejrup LB, Pedersen MF (2012) The effect of temporal variability in salinity on the invasive red alga *Gracilaria vermiculophylla*. *Eur J Phycol* 47:254–263
- Nettleton JC, Mathieson AC, Thornber C, Neefus CD, Yarish C (2013) Introductions of *Gracilaria vermiculophylla* (Rhodophyta, Gracilariaceae) to New England, USA: estimated arrival times and current distribution. *Rhodora* 115:28–41
- Newton C, Bracken MES, McConville M, Rodrigue K, Thornber CS (2013a) Invasion of the red seaweed *Heterosiphonia japonica* spans biogeographic provinces in the western North Atlantic Ocean. *PLoS ONE* 8(4):e62661
- Newton C, Guidone M, Thornber CS (2013b) Impacts of invasive *Gracilaria vermiculophylla* on the reproductive ecology of

- native benthic invertebrates. SICB Annual Meeting 2013, January 3–7, 2013, San Francisco, CA, USA
- Nyberg CD (2007) Introduced marine macroalgae and habitat modifiers: the ecological role and significant attributes. Doctoral thesis, Department of Marine Ecology, Goteborg University, Goteborg, Sweden
- Nyberg CD, Wallentinus I (2005) Can species traits be used to predict marine macroalgal introductions? *Biol Invasions* 7:265–279
- Nyberg CD, Wallentinus I (2009) Long-term survival of an introduced red alga in adverse conditions. *Mar Biol Res* 5:304–308
- Nyberg CD, Thomsen MS, Wallentinus I (2009) Flora and fauna associated with the introduced red alga *Gracilaria vermiculophylla*. *Eur J Phycol* 44:395–403
- Nylund GM, Weinberger F, Rempt M, Pohnert G (2011) Metabolomic assessment of induced and activated chemical defence in the invasive red alga *Gracilaria vermiculophylla*. *PLoS ONE* 6(12):e29359
- Ohmi H (1956) Contributions to the Knowledge of Gracilariaceae from Japan, II: on a new species of the genus *Gracilariopsis*, with some considerations on its ecology. *Bull Fac Fish Hokkaido Univ* 6:271–279
- Orth RJ, Olyarnik S, Short FT, Waycott M, Williams SL, Caruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes RA, Kendrick GA, Kenworthy JW (2006) A global crisis for seagrass ecosystems. *Bioscience* 56(12):987–996
- Pérez JE, Nirchio M, Alfonsi C, Munoz C (2006) The biology of invasions: the genetic adaptation paradox. *Biol Invasions* 8:1115–1121
- Pinon-Gimate A, Serviere-Zaragoza E, Ochoa-Izaguirre MJ, Páez-Osuna F (2008) Species composition and seasonal changes in macroalgal blooms in lagoons along the southeastern Gulf of California. *Bot Mar* 51:112–123
- Prentis PJ, Wilson JR, Dormontt EE, Richardson DM, Lowe AJ (2008) Adaptive evolution in invasive species. *Trends Plant Sci* 13:288–294
- Prentis PJ, Woolfit M, Thomas-Hall SR, Ortiz-Barrientos D, Pavašovic A, Lowe AJ, Schenk PM (2010) Massive ly-paralleling sequencing and analysis of expressed sequence tags in a successful invasive plant. *Ann Bot (London)* 106:1009–1017
- Raïkar S, Iima M, Fujita Y (2001) Effect of temperature, salinity and light intensity on the growth of *Gracilaria* spp. (Gracilariales, Rhodophyta) from Japan, Malaysia and India. *Indian J Mar Sci* 30:98–104
- Rempt M, Weinberger F, Grosser K, Pohnert G (2012) Conserved and species-specific oxylipin pathways in the wound-activated chemical defense of the noninvasive red alga *Gracilaria chilensis* and the invasive *Gracilaria vermiculophylla*. *Beilstein J Org Chem* 8:283–289
- Roleda MY, Nyberg CD, Wulff A (2012) UVR defense mechanisms in eurytopic and invasive *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta). *Physiol Plantarum* 146:205–216
- Rueness J (2005) Life histories and molecular sequences of *Gracilaria vermiculophylla*. *Phycologia* 44:120–128
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Ann Rev Ecol Syst* 32:305–332
- Saunders GW (2009) Routine DNA barcoding of Canadian Gracilariales (Rhodophyta) reveals the invasive species *Gracilaria vermiculophylla* in British Columbia. *Mol Ecol Res* 9:141–150
- Schaffelke B, Smith JE, Hewitt CL (2006) Introduced macroalgae—a growing concern. *J Appl Phycol* 18:529–541
- Schrey AW, Coon CAC, Grispo MT, Award M, Imboma T, McCoy ED, Mushinsky HR, Richard CL, Martin LB (2012) Epigenetic variation may compensate for decreased genetic variation with introductions: a case study using house sparrows (*Passer domesticus*) on two continents. *Genet Res Int* doi:10.1155/2012/979751
- Sfriso A, Maistro S, Andreoli C, Moro I (2010) First record of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta) in the Po Delta Lagoons, Mediterranean Sea (Italy). *J Phycol* 46:1024–1027
- Staehr PA, Pedersen MF, Thomsen MS, Wernberg T, Krause-Jensen D (2000) Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. *Mar Ecol Prog Ser* 207:79–88
- Teso SV, Bigatti G, Casas GN, Piriz ML, Penchaszadeh PE (2009) Do native grazers from Patagonia, Argentina, consume the invasive kelp *Undaria pinnatifida*? *Rev Mus Argentino Cienc Nat* 11(1):7–14
- Thomsen MS (2010) Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. *Aquat Invasions* 5:341–346
- Thomsen MS, McGlathery KJ (2005) Facilitation of macroalgae by the sedimentary tube forming polychaete *Diopatra cuprea*. *Estuar Coast Shelf Sci* 62:63–73
- Thomsen MS, McGlathery KJ (2007) Stress tolerance of the invasive macroalgae *Codium fragile* and *Gracilaria vermiculophylla* in a soft-bottom turbid lagoon. *Biol Invasions* 9:499–513
- Thomsen MS, Gurgel CFD, Fredericq S, McGlathery KJ (2005) *Gracilaria vermiculophylla* (Rhodophyta, Gracilariales) in Hog Island Bay, Virginia: a cryptic alien and invasive macroalga and taxonomic correction. *J Phycol* 42:139–141
- Thomsen MS, McGlathery KJ, Tyler AC (2006) Macroalgal distribution patterns in a shallow, soft-bottom lagoon, with emphasis on the non-native *Gracilaria vermiculophylla* and *Codium fragile*. *Estuar Coast* 29:465–473
- Thomsen MS, Stehr P, Nyberg CD, Krause-Jensen D, Schwaeter S, Silliman BR (2007) *Gracilaria vermiculophylla* in northern Europe, with focus on Denmark, and what to expect in the future. *Aquat Invasions* 3:1–12
- Thomsen MS, Wernberg T, Tuya F, Silliman BR (2009a) Evidence for impacts of nonindigenous macroalgae: a meta-analysis of experimental field studies. *J Phycol* 45(4):812–819
- Thomsen MS, McGlathery KJ, Schartschild A, Silliman BR (2009b) Distribution and ecological role of the nonnative macroalga *Gracilaria vermiculophylla* in Virginia salt marshes. *Biol Invasions* 11:2303–2316
- Tyler AC, McGlathery KJ (2006) Uptake and release of nitrogen by the macroalgae *Gracilaria vermiculophylla* (Rhodophyta). *J Phycol* 42:515–525
- Tyler AC, McGlathery KJ, Macko SA (2005) Uptake of urea and amino acids by the macroalgae *Ulva lactuca* (Chlorophyta)

- and *Gracilaria vermiculophylla* (Rhodophyta). *Mar Ecol Prog Ser* 294:161–172
- Weinberger F, Buchholz B, Karez R, Wahl M (2008) The invasive red alga *Gracilaria vermiculophylla* in the Baltic Sea: adaptation to brackish water may compensate for light limitation. *Aquat Biol* 3:251–264
- Williams SL, Smith JE (2007) A global review of the distribution, taxonomy, and impacts of introduced seaweeds. *Ann Rev Ecol Syst* 38:327–359
- Yokoya NS, Kakita H, Obika H, Kitamura T (1999) Effects of environmental factors and plant growth regulators on growth of the red alga *Gracilaria vermiculophylla* from Shikoku Island, Japan. *Hydrobiologia* 399:339–347
- Yoshida T, Yoshinaga K, Nakajima Y (1995) Check list of marine algae of Japan. *Jpn J Phycol* 43:115–171