

UHI Research Database pdf download summary

Exploring, harnessing and conserving marine genetic resources towards a sustainable seaweed aquaculture

Brakel, Janina; Sibonga, Rema C.; Dumilag, Richard V.; Montalescot, Valeria; Campbell, Iona; Cottier-cook, Elizabeth J.; Ward, Georgia; Le Masson, Virginie; Liu, Tao; Msuya, Flower E.; Brodie, Juliet; Lim, Phaik-eem; Gachon, Claire M. M.

Published in:

Plants, People, Planet

Publication date:

2021

The re-use license for this item is:

CC BY

The Document Version you have downloaded here is:

Publisher's PDF, also known as Version of record

The final published version is available direct from the publisher website at:
[10.1002/ppp3.10190](https://doi.org/10.1002/ppp3.10190)

[Link to author version on UHI Research Database](#)

Citation for published version (APA):

Brakel, J., Sibonga, R. C., Dumilag, R. V., Montalescot, V., Campbell, I., Cottier-cook, E. J., Ward, G., Le Masson, V., Liu, T., Msuya, F. E., Brodie, J., Lim, P., & Gachon, C. M. M. (2021). Exploring, harnessing and conserving marine genetic resources towards a sustainable seaweed aquaculture. *Plants, People, Planet*, 3(4), 337-349. <https://doi.org/10.1002/ppp3.10190>

General rights

Copyright and moral rights for the publications made accessible in the UHI Research Database are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights:





- 1) Users may download and print one copy of any publication from the UHI Research Database for the purpose of private study or research.
- 2) You may not further distribute the material or use it for any profit-making activity or commercial gain
- 3) You may freely distribute the URL identifying the publication in the UHI Research Database

Take down policy

If you believe that this document breaches copyright please contact us at RO@uhi.ac.uk providing details; we will remove access to the work immediately and investigate your claim.

REVIEW

Exploring, harnessing and conserving marine genetic resources towards a sustainable seaweed aquaculture

Janina Brakel¹ | Rema C. Sibonga^{2,3} | Richard V. Dumilag⁴  | Valeria Montalescot¹ | Iona Campbell¹ | Elizabeth J. Cottier-Cook¹ | Georgia Ward^{5,6} | Virginie Le Masson⁷ | Tao Liu^{8,9} | Flower E. Msuya¹⁰  | Juliet Brodie⁵  | Phaik-Eem Lim¹¹ | Claire M. M. Gachon^{1,12} 

¹Scottish Association for Marine Science, Scottish Marine Institute, Oban, United Kingdom

²Institute of Aquaculture, College of Fisheries and Ocean Sciences, University of the Philippines Visayas, Iloilo, Philippines

³Aquaculture Department, Southeast Asian Fisheries Development Centre, Iloilo, Philippines

⁴Institute of Oceanography and Environmental Science, Mindanao State University, Tawi-Tawi College of Technology and Oceanography, Bohoh Sallang, Sanga-Sanga, Bongao, Tawi-Tawi, Philippines

⁵Department of Life Sciences, Natural History Museum, London, UK

⁶Centre for Environment, Fisheries and Aquaculture Science (Cefas), Weymouth Laboratory, Weymouth, Dorset, United Kingdom

⁷IRDR Centre for Gender and Disaster, University College London, London, United Kingdom

⁸College of Marine Life Science, Ocean University of China, Qingdao, Shandong Province, People's Republic of China

⁹School of Marine Science, Sun Yat-Sen University, Zhuhai, Guangdong Province, People's Republic of China

¹⁰University of Dar es Salaam, Dar es Salaam, Tanzania

¹¹Institute of Ocean and Earth Sciences, University of Malaya, Kuala Lumpur, Malaysia

¹²UMR 7245 - Molécules de Communication et Adaptation des Micro-organismes, Muséum National d'Histoire Naturelle, CNRS, Paris, France

Correspondence

Claire M. M. Gachon, Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA37 1QA, United Kingdom.
Email: claire.gachon@sams.ac.uk

Funding information

United Kingdom Research and Innovation–Global Challenges Research Fund (UKRI–GCRF), Grant/Award Number: BB/P027806/1; Department of Science and Technology (DOST), Philippine Council for Agriculture, Aquatic, and Natural Resources Research and Development (PCAARRD)

Societal Impact Statement

Seaweed cultivation is the fastest-growing aquaculture sector, with a demonstrable potential to drive development in some of the poorest coastal populations worldwide. However, sustainable exploitation, fair access and equitable benefits from marine genetic resources, such as seaweeds have yet to be fully realised. Patchy fundamental knowledge on the genetic diversity and metabolic potential of algae limits their exploitation; scant practical skills and low investment in breeding restricts germplasm availability and the Nagoya protocol has only partially remediated insufficient governance. Further developments and the addressing of knowledge gaps in relation to biosecurity, breeders' rights and conservation of genetic resources are needed for progress.

Summary

We review how seaweed genetic resources are currently used in aquaculture, in relation to the diversification and rapidly increasing use of marine resources. Using a revealing case-study, we summarise the potential for positive societal change, underpinned by the cultivation of eucheumatoid carrageenophytes (species of the red algal

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors, *Plants, People, Planet* © New Phytologist Foundation

genera *Eucheuma* and *Kappaphycus*), an activity which has been successfully initiated in many tropical countries to support their economic development. We also review the challenges currently faced by this industry and identify potential threats to the seaweed cultivation sector. Accordingly, we suggest new directions to support the continued development of an economically resilient and environmentally sustainable industry based on the utilisation of genetic resources.

KEYWORDS

algae, aquaculture, biosecurity, breeding, genetic diversity, marine genetic resources

1 | INTRODUCTION

Marine ecosystems are a widely recognised reservoir of underexploited genetic resources (Arnaud-Haond et al., 2011) the phylogenetic breadth of which exceeds that of terrestrial ecosystems (Costello & Chaudhary, 2017). A wealth of novel diversity, revealed through large-scale marine meta-barcoding projects, not only awaits to be described (de Vargas et al., 2015), but its genetic and metabolic potential also requires characterisation. The imbalance of knowledge between terrestrial and marine organisms is illustrated by the low proportion of functionally annotated genes in the few available genomes of marine organisms, for example, brown algae (Dittami et al., 2020) or corals (Cleves et al., 2020). Several authors have recently called for the urgent development of a suitable governance structure to protect the intellectual property of innovators, yet refraining unequitable appropriation of marine genetic resources (Blasiak et al., 2018; Vanagt et al., 2019), to guarantee the

conservation of biodiversity (Diz, 2018), and if traded, to promote good biosecurity practice (Campbell et al., 2019).

Amongst all marine resources, algae have a long-recognised, yet still underutilised, potential for human use and biotechnological applications (Arrieta et al., 2010). Driven by increasing demand and multiple potential uses as feed, food, pharmaceuticals or nutraceuticals, aquaculture especially of marine macroalgae, that is, seaweeds has been developing at an unprecedented pace (FAO, 2020). Between 2010 and 2018, global production of red and brown seaweeds increased by 89.5% of the total 31.3 million metric tonnes wet weight, representing a value of 12.4 billion US \$ (Table 1). Despite a downturn in biomass production in 2017 and 2018, a considerable proportion of the global seaweed production is due to the expanding cultivation of the red algal genera *Kappaphycus* and *Eucheuma* (herein referred to as eucheumatoids) in Southeast Asia and the Western Indian Ocean, especially in Indonesia (FAO, 2020). Seaweed aquaculture has become an important industry that provides jobs and livelihoods to millions of families in rural coastal communities,

TABLE 1 Global production of the main seaweed crops from 2010 to 2018, in quantity and value (FAO, 2020), and number of registered varieties in China, Korea and Japan (mostly Hwang et al., 2019, Plant Variety Database accessed June 2020, UPOV, but see Table S1)

	Production in metric tonnes fresh weight		Value in billion USD		No. of certified varieties*	
	2010	2018**	2010	2018**	2010	2018**
Red algae	8.3	17.3 (+105.7%)	3.6	6.3 (+74.6%)	7	31 (+343%)
Foliose Bangiales (<i>Neoporphyra haitanensis</i> & <i>Neopyropia</i> spp.)	1.6	2.9 (+78.9%)	1.8	2.8 (+59.9%)	6	28 (+367%)
Gracilarioids (sensu lato)	1.1	3.3 (+192%)	0.4	1.9 (+336%)	1	3 (+200%)
Eucheumatoids (<i>Eucheuma denticulatum</i> and <i>Kappaphycus</i> spp.)	5.6	11.1 (+95%)	1.4	1.6 (+14%)	NRV	NRV
Brown algae	8.1	14.0 (+72.7%)	3.2	6.1 (+89.6%)	5	18 (+260%)
<i>Undaria pinnatifida</i>	1.5	2.3 (+54.1%)	0.7	1.6 (117.8%)	0	7
<i>Saccharina</i> spp.	6.5	11.4 (75.4%)	2.4	4.3 (+77.0%)	5	11 (+120%)
<i>Sargassum</i> spp.	0.10	0.27 (+177.1%)	0.061	0.213 (+347.1%)	NRV	NRV
Overall sum	16.4	31.3 (+89.5%)	6.8	12.4 (+81.7%)	12	49 (+308%)

Abbreviation: NRV, No registered varieties.

*Data presented for Korea, Japan and China, which represent 64% of the global production in 2018.

**Values in bracket correspond to the % increase between 2010 and 2018.

particularly in areas where few other opportunities exist, including enabling women to be economically active and gain independent economic power (Msuya & Hurtado, 2017; Rebours et al., 2014). Seaweeds consumed as sea vegetables, especially nori (*Neopyropia/Neoporphyra*) are valuable protein resources for human nutrition (Fleurence, 2004). They are also used in animal feed, for example in polyculture or integrated multi-trophic aquaculture systems to help meet the global demand for dietary protein and to contribute to global food security, aligning with several UN Sustainable Development Goals (Bjerregaard et al., 2016). As seaweed aquaculture is predicted to increase significantly, the growth of an economically and environmentally sustainable industry would create major opportunities for coastal communities and subsequently, contribute to poverty reduction (Cottier-Cook et al., 2016).

Taking the cultivation of eucheumatoid algae as a case-study, Box 1 highlights the intricate agronomical, ecological and societal challenges that need to be tackled to achieve resilient production systems, mitigate their potential impact on ecosystems and provide stable income and prospects for people working in this industry. Many other domesticated seaweed species face similar challenges, such as a narrow genetic diversity of cultivars (e.g. Guillemain et al., 2008), an increased frequency of diseases and pests (Loureiro et al., 2015), gene flow between farms and wild populations (Grulois et al., 2011), as well as limited or inadequate governance (Campbell et al., 2019). A common theme underlying many of these issues, is the management of genetic resources and the requirement to develop robust regional, national and supranational governance towards their conservation, as well as their equitable and sustainable exploitation. New technology opens novel avenues to explore the genetic potential of seaweed resources, whether they are already cultivated or not. Here, we review the current exploitation of seaweed genetic resources and their governance in the context of a growing aquaculture sector, identify knowledge gaps and explore new directions underpinning the continued development of a sustainable and resilient seaweed aquaculture industry that aligns with major sustainable development goals.

2 | CURRENT FRONTIERS IN THE EXPLOITATION OF ALGAL GENETIC RESOURCES

Genetic resources, breeding concepts and the resistance of seaweeds against stressors are far less studied than in major land-based crops, most of which have a long-standing research and biobanking history (Tanksley & McCouch, 1997). Although seaweeds have been traditionally used for millennia throughout the world, their large-scale cultivation only dates back a few decades in most countries and, consequently the impacts of their domestication have only been investigated more recently (e.g. Loureiro et al., 2015; Valero et al., 2017 and references therein). Intra-specific genetic diversity is widely recognised as the basis for species' survival, adaptation potential and resistance against biotic and abiotic stressors, and

thus forms the foundation for sustainable cultivation and stable ecosystems (Laikre et al., 2020). Efforts to characterise and identify these genetic resources of wild seaweed populations and cultivars have been accelerated lately, for example, in kelps (e.g. Guzinski et al., 2016; Zhang et al., 2017), *Undaria pinnatifida* (Guzinski et al., 2018; Shan et al., 2018), *Sargassum* (Le Cam et al., 2019) and *Agarophyton* (Guillemin et al., 2008, 2014). Until recently, population genetic studies primarily targeted ecologically important algae of temperate or cold waters and aimed to reconstruct their paleo-geographic histories (Hu et al., 2016). Studies aimed at underpinning breeding efforts, however, have only been initiated in recent years and knowledge is particularly limited for tropical species. In fact, cryptic diversities in many seaweed groups have only recently started to reveal their breadth, with the aid of molecular data, including groups of major economic interest, such as the eucheumatoids (Lim et al., 2017, see also Box 1) and foliose Bangiales (Yang et al., 2020).

A key challenge to enable cultivation and breeding is to control the reproduction and life history of seaweeds; indeed, the development of such knowledge is a milestone of domestication (Valero et al., 2017 and references therein). Red and brown algae exhibit diverse and complex, bi- or tri-phasic life histories, many of which have only been recently described or remain imperfectly known. Investigations into sex determination (Shan et al., 2015; Umen & Coelho, 2019; Zhang et al., 2015), life history transition control (Cock et al., 2014) and parthenogenesis (Mignerot et al., 2019) are fundamental resources for breeding efforts (Lipinska et al., 2015). While progress has been steady for brown algae, key knowledge gaps remain. For example, the genetic determinants of sex in red algae have yet to be identified. Similarly, the recent discovery of co-existing polyploidy (triploids, tetraploids and mixoploids) in gametophytes of three *Porphyra* species challenges the conventional wisdom that the gametophytes are necessarily haploid; the co-existence of several mating types in wild *Porphyra* populations underlines our paucity in knowledge of the intra-specific diversity of life histories and their ecological significance (Varela-Álvarez et al., 2018).

Bearing in mind this diversity of seaweed life histories, specific methods to biobank germplasm and produce quality seed-stock still need to be developed for each cultivated species. Cost-effective biobanking typically requires the maintenance of small, easily cultivable life stages with indefinite growth. Seed-stock production, however, often requires cost-effective amplification of healthy germplasm of high, predictable agronomic quality. Similar to animals and plants, the strategies of choice differ between sexually reproducing seaweeds (e.g. kelps) and those that can be propagated asexually, be it through parthenogenesis, apomixy or cuttings (e.g. eucheumatoids, see details in Box 1). For sexually reproducing species, an important research focus is to control life history transitions or exploit natural plasticity of life histories (Maggs, 1988) and to find individuals able to propagate asexually, to facilitate biobanking and germplasm amplification (Ichiara et al., 2019; Li et al., 2017; Takahashi & Mikami, 2017). Comparable to crops such as banana and potato, asexually reproducing seaweeds are far easier to propagate; however, the development of new cultivars

still relies on the identification of agronomically valuable individuals in the wild, or on the ability to perform controlled crossings. Finally, and again similar to some land crops and cultured animals (e.g. oyster and salmon), the control of ploidy, whether through endo-polyploidisation, allo-polyploidisation or the generation of somatic hybrids offers hope for yield improvement and for the control of the genetic pollution of wild stocks by escapees (Goecke et al., 2020). Much can be learned from elaborate strategies deployed in animals and plants, as well as their pitfalls, particularly the dramatic erosion of genetic diversity that has plagued agriculture and animal aquaculture since the last century (Hainzelin, 2013).

Novel DNA sequencing and analytical technologies provide potential opportunities to develop efficient pipelines for a large-scale, systematic exploration of the genetic and metabolic potential of algae that can aid further biotechnological exploitation. Although it is yet to be applied at scale in seaweeds, genome breeding has demonstrably shown its potential to accelerate the introgression in crops of genetic regions encoding high performance traits or increased resistance against abiotic and biotic stressors (Hickey et al., 2017). In addition to the potential of multi-omic approaches to improve crops for long-established uses of seaweeds, the exploration of novel species for cultivation, or discovery of novel bioactive compounds is also tantalising (Kumar et al., 2016). This general trend certainly contributes to the exponential growth of the number of marine species undergoing domestication (Duarte et al., 2007), and should be further explored for seaweeds. However, with over 95% of seaweed cultivation activities taking place in low- or middle-income countries, significant investment and capacity building are needed to harness this scientific potential and ensure that seaweed farmers benefit fairly (Cottier-Cook et al., 2016).

3 | NOVEL CONSERVATION CHALLENGES BROUGHT BY ALGAL CULTIVATION

The accelerated loss of marine biodiversity is a general concern (Worm et al., 2006). Key seaweed-dominated ecosystems are disappearing worldwide (Arafeh-Dalmau et al., 2020; Smale, 2020). Global warming, ocean acidification, eutrophication and other anthropogenic pressures are key drivers for rapid changes of seaweed-dominated ecosystems and their poleward shift or even retraction (Brodie, Williamson, et al., 2014; Fabricius et al., 2015; Wernberg et al., 2016). Physiological responses of tropical seaweeds to warming and ecological responses to climate change are only starting to be understood (Kumar et al., 2020). Monitoring change and diversity loss in the marine environments continues to be a challenge, leading to the concern that vanishing tropical seaweed populations remain largely unnoticed.

In addition to these global drivers, rapid development of cultivation incurs novel risks for seaweeds in temperate as in tropical regions, which are only beginning to be identified. For most species, very little is known about the relative abundance of gametophytes as opposed to sporophytes in wild stocks, the balance between sexual versus vegetative reproduction, or ploidy (as reported above

for *Porphyra*, for example). Some microscopic life stages, such as the gametophytes of kelps are elusive in the field, resulting in a paucity of data about their ecology, longevity and vulnerability to environmental stressors or changes (Coleman & Goold, 2019). It is clear, however, that the control exerted over the life history and ploidy by farmers might shift the balance between life stages and reproductive modes in the field, with consequences on the genetic structure of populations and their resilience to perturbations. In the most comprehensively studied species, the agar-producing alga *Agarophyton chilense* (formerly *Gracilaria chilensis*) is predominantly propagated vegetatively by farmers and farming practices favour the propagation of diploid tetrasporophytes over haploid gametophytes (Guillemin et al., 2008). Evidence suggests that over-harvesting of wild stocks, in combination with the vegetative propagation in farms, has resulted in an extreme impoverishment of the species' genetic diversity in Chile (Guillemin et al., 2014).

To date, seaweed cultivation has been widely regarded as environmentally benign, because the ability of seaweeds to absorb nutrients helps remediate eutrophication caused, for example, by fish or shellfish aquaculture (Neori et al., 2004). Seaweed cultivation also provides some economic incentive for coastal populations to disengage from environmentally harmful practices, such as dynamite fishing or over-fishing (Ask et al., 2003; Msuya & Porter, 2014). However, many cultivation attempts have relied on the introduction of non-native germplasm (e.g. for eucheumatoids, see details in Box 1). With the exception of a few exemplary cases (Araújo et al., 2020), only limited environmental monitoring has been performed alongside these cultivation attempts and it typically ceases when farms are abandoned (Sellers et al., 2015). Yet, there are examples where non-native eucheumatoids have become established in the vicinity of farms, for example in Tanzania (Halling et al., 2013; Tano et al., 2015). The morphological plasticity of many seaweeds and the difficulty to identify them in the field also contributes to unnoticed introductions for many years. For example, the first reports of introduced eucheumatoids escaping farms and of their subsequent establishment in the wild were largely made 10 to 20 years after cultivation was initiated in the area (Figure 1). This might be due to limited environmental monitoring, but also an indication of the time-scale necessary for such an impact to become detectable (Figure 1). It should be emphasised that agriculture and non-native species are major drivers of species extinction on land (Bellard et al., 2016). Therefore, the scale at which the global seaweed cultivation progresses and its integration with other human activities arguably calls for a careful assessment of its potential long-term impacts on coastal ecosystems and their possible mitigation (Eggertsen & Halling, 2020). The specific characteristics of seaweeds, such as their complex life histories, would need to be fully considered when performing risk assessments for invasiveness (Krueger-Hadfield, 2019).

Although still poorly documented for algae (Loureiro et al., 2015, see also Box 1), the worsening of disease outbreaks due to the intensification and un-intentional translocation of pathogens, alongside the trade of seed stock, are well-known issues in other aquaculture sectors, for example, salmon (Johansen et al., 2011), crustaceans (Stentiford et al., 2012) and oysters (Mineur et al., 2014). For instance,

farmers and breeders are still in their infancy (Wade et al., 2020). Over the last few years, however, there has been a sharp rise of seaweed varieties registered with the International Union for the Protection of New Varieties of Plants (UPOV, Table 1). While the UPOV system provides protection to breeders and should thus encourage investment, it is important to note that it has been widely seen as encouraging homogeneous crops and subsequent loss of genetic diversity (Ahmadi et al., 2013). Also, only a few governments currently engage with UPOV for seaweeds (e.g. Japan and Korea). This reflects a continuing global imbalance among the countries involved in seaweed production and those engaged in research and biotechnology markets (Mazarrasa et al., 2013). Accordingly, this poses long-term challenges concerning the establishment of sustainable and equitable international partnerships. It is, therefore, important to accompany the current development of the industry with a reflection on value-chains and power balance locally, nationally and internationally. For example, the development of micropropagation for eucheumatoids to mass-produce germplasm free of key pathogens could be accompanied by participatory breeding initiatives that involve local farmers, for which the current small-scale family farming would be a favourable setting. Such initiatives would encourage the maintenance of genetic diversity, select local adaptations in the context of climate change and empower local farming communities to keep ownership of their algal seed-stock.

The sustainable exploitation of seaweed genetic resources also requires the implementation of effective marine conservation policies. Despite new technical developments, such as eDNA barcoding with primers targeting specific groups of seaweeds (Stat et al., 2017) underwater monitoring remains a challenge and the conservation status of many seaweeds remains imperfectly known. Accordingly, only a minute proportion of seaweeds are listed in the global IUCN red lists and most of these have deficient data available to assess their conservation status (Table 2), although it is worth mentioning initiatives to generate red data lists for seaweeds on national level, (e.g. Brodie et al., 2014), under-pinning the efforts to implement management regimes. To specifically ensure that seaweed cultivation does not impair persistence of wild seaweed populations, adaptable and reactive biosecurity policies must accompany the development of seaweed aquaculture and thereby avoiding experiences made in other aquaculture such as genetic introgression of

cultivated genetic material into wild populations or pathogen spill-over threatening the wild populations (Badis et al., 2019). To avoid these negative impacts of seaweed aquaculture rigorous monitoring, innovation and adaptable and reactive policies, and communication between stakeholders, scientists and legal authorities are required.

5 | CONCLUSION AND PERSPECTIVES

Several initiatives, such as one launched by the Food and Agriculture Organization of the United Nations in 2019 to assess aquatic genetic resources, widely reflect an increase in the awareness of the potential economic value of marine genetic resources (FAO, 2019). Here, we have highlighted the challenges faced by the seaweed producing industry by focusing on the carrageenan-producing eucheumatoids. However, many more seaweed taxa contain widely known, although hitherto barely exploited bioactive metabolites with anti-cancer, anti-viral, anti-tumour, hypocholesterolemic or hypolipidemic properties (Holdt & Kraan, 2011; Torres et al., 2019), which are driving a rapid diversification of the species undergoing cultivation attempts.

To support coastal communities to exploit seaweed genetic resources for example by accessing more resilient cultivars, diversification of cultivated species and potentially, accessing high value seaweed-derived products, scientific efforts and development initiatives must build and rely on collaboration with farmers and coastal communities. The integration of their traditional knowledge and the genetic resources that they manage or own is vital when designing breeding programmes or developing strategies to manage disease and pest outbreaks, for example. Innovative solutions are requested that balance the need to reduce the risk to endemic wild seaweed populations from seaweed farming and allow the industry to expand in an economically and environmentally sustainable way, while being inclusive of the local community. Integration of scientific insight and traditional knowledge of local communities needs to inform policies that address sustainable challenges more holistically (i.e. by understanding the agronomical, ecological and societal dimension of marine farming). To this end, national implementation of policy frameworks that regulate access, biosecurity and benefit sharing must be context-specific.

TABLE 2 Number of species assessed for their conservation status in the IUCN red lists

Group	Estimate of described species	Number of species evaluated	Data Deficient	Least Concern	Near Threatened	Vulnerable	Endangered	Critically endangered	Extinct
Red algae	7,349*	58	44	4	0	0	0	6	1
Brown algae	2,065*	15	9	0	0	1	1	4	0
Green algae	6,734*	2	2	0	0	0	0	0	0
Vertebrates	72,478**	52,649							
Invertebrates	1,504,341**	23,808							
Flowering plants	369,000**	43,557							

*Number of species in Algaebase (accessed Sept 2020).

**IUCN Red list Statistics Version 2020–2 Table 1a.

BOX 1 Eucheumatoid cultivation—a case-study of a globalised, vegetatively propagated crop that supports development of deprived coastal communities

Eucheumatoids are sought after for their rich content of kappa and iota carrageenans (Lim et al., 2017). Carrageen is used as an additive in manufactured food or as a stabiliser in cosmetics. Driven by high demand and over-exploitation of wild stocks, commercial cultivation of eucheumatoids was initiated in the Philippines in 1969 (Hurtado et al., 2014, Figure 1). Subsequently, cultivation was introduced in neighbouring countries in Asia, the Western Indian Ocean and the Americas, predominantly Brazil. Today, about 43 countries are engaged, or have been engaged in the cultivation of eucheumatoids (Kelly et al., 2020). Their annual production is 10.3 metric tonnes of fresh weight, for an output worth approximately 1 billion US \$ (2017, FAO Fisheries statistics). Eucheumatoid farming is a major economic opportunity, specifically for low-income or middle-income regions, with proactive government policies in place, for example in Indonesia, Malaysia, the Philippines and Tanzania. Despite concerns about over-production, price stagnation (Table 1) and a controversy about carrageenan safety as a human food ingredient (Martino et al., 2017), this industry has enabled women to become economically active (Msuya, 2006), and offers livelihood opportunities to poor, often displaced populations, particularly in Asia (Nimmo, 1986; Nor et al., 2017).

From 37 extant eucheumatoid species (belonging to the genera *Eucheuma*, *Kappaphycus*, *Betaphycus*, *Mimica*, *Eucheumatopsis* and *Tacanoosca*) worldwide, two species dominate the market (*Kappaphycus alvarezii* and *Eucheuma denticulatum*), of which a few haplotypes have been introduced globally for cultivation (see Figure 2a,b; Halling et al., 2013; Zuccarello et al., 2006). *Kappaphycus striatus* considerably contributes to cultivation, particularly in South East Asian farms (Hurtado et al., 2016, Figure 2c); *K. malesianus* is only cultivated within the borders of Malaysia and the Philippines (Figure 2d). Vegetative propagation is the standard practise in eucheumatoid farming, similar to potato and banana. In contrast to the global distribution of a few haplotypes, a large number of locally recognised varieties are cultivated in their native area, in the Philippines, Malaysia and Indonesia (Hurtado et al., 2016; Quiaoit et al., 2016; Tan et al., 2013). Considerable plasticity in the morphology of eucheumatoids, however, impedes species identification. Varieties, which have been gathered from wild populations, are given vernacular names by seaweed farmers. These local vernacular names are not unified between different regions and often farmers are unaware of the actual species that they are cultivating (Dumilag et al., 2016a; Ganson-Fortes et al., 2012; Montes et al., 2008; Tan et al., 2013). This limitation in the ability to identify taxa and in the genetic characterisation of currently cultivated eucheumatoids is, therefore, a problem for the entire sector. Farmers receive lower prices for their product if they inadvertently mix species producing different types of carrageenans as *Kappaphycus* spp. contain the higher valued kappa carrageenan, while *Eucheuma denticulatum* contains the lower priced iota carrageenan; it impedes their conscious decision in cultivar choice and also restricts supra-regional management of cultivar diversity, for example, in the establishment of biobanks.

Another serious concern is the widespread, and apparently worsening, occurrence of diseases, particularly 'ice-ice' disease and infestations by filamentous red algal endo-epiphytes (Hurtado et al., 2006; Largo, 2002; Vairappan et al., 2008). 'Ice-ice' is characterised by a whitening or loss of pigmentation of the thallus, followed by the disintegration of affected tissues and often the detachment of plants from cultivation ropes, resulting in loss of biomass. The condition appears to be the result of complex interactions between abiotic stress induced by 'unfavourable' shifts in environmental parameters, particularly a decrease in salinity or irradiance or an increase in water temperature or pH (e.g. Alibon et al., 2019; Largo et al., 1995) and the proliferation of 'ice-ice' promoting bacteria (often identified as *Vibrio* or *Pseudomonas* (Azizi et al., 2018; Largo et al., 1995) and it is thought to affect all cultivated eucheumatoid varieties (Sade et al., 2006; Tisera & Naguit, 2009). Infestation with epiphytic filamentous red algae is mostly caused by species of the genera *Melanthamnus* (previously *Neosiphonia/Polysiphonia*), *Ceramium*, *Acanthophora*, *Centroceras* and *Colaconema* (Araújo et al., 2014; Bustamante et al., 2015; Hurtado et al., 2006; Largo, 2002; Largo et al., 2020; Tsiresy et al., 2016; Vairappan et al., 2008). In some areas, prevailing diseases and pests have forced farmers to cease their activity. For example, in Tanzania, the production of *K. alvarezii* collapsed from 1,000 metric tonnes fresh weight in 2001 to ca. 13 metric tonnes fresh weight in 2010 and in Madagascar, it dropped from 1,860 metric tonnes fresh weight in 2009 to 110 metric tonnes fresh weight in 2012 (Msuya et al., 2014). Figure 1 illustrates the generality of this trend and shows how—after an initial highly profitable period of up to ten years following the successful introduction of farming—isolated disease outbreaks are typically reported, quickly followed by regional outbreaks. Diseases are usually mitigated by switching to other cultivars, changing the location of farms seasonally, or stopping farming temporarily during the 'disease' season. Yet, production is still reduced by disease and pest outbreaks and the extent by which the mostly uncontrolled globalised movement of germplasm may, or not, have contributed to the onset and worsening of these outbreaks is unknown.

In the light of these issues, there is a strong need for breeding programmes that produce disease-resistant cultivars that can tolerate the higher temperatures as a consequence of climate change and the provision of farmers with pest-free germplasm after a disease outbreak. Completing the entire life cycle of eucheumatoids in a laboratory, however, has only been achieved at a small scale (Luhan &

BOX 1 (Continued)

Sollesta, 2010). The successful application of micropropagation techniques offers new hope to establish biobanks from wild individuals (Luhan & Mateo, 2017); however, the depletion of wild eucheumatoid stocks is a matter of concern. Alarmingly, our knowledge on the conservation status of any of the cultivated eucheumatoid species is highly limited. Figure 2 provides an overview of available molecular data for the four cultivated eucheumatoid species. It shows a bias towards the molecular characterisation of farmed individuals; additionally, the overall sampling depth is insufficient to assess the genetic structure of wild populations. Throughout the assumed native ranges, there are also numerous reports of over-harvest prior to cultivation (Mshigeni, 1984; Trono, 1999), of vanishing populations, presumably as a result of global warming, and some reports of cryptic invasion of farmed genotypes into wild populations (Dumilag et al., 2016; Halling et al., 2013; Tano et al., 2015). All these factors may contribute to the rarefaction of wild stocks and potentially, their genetic impoverishment.

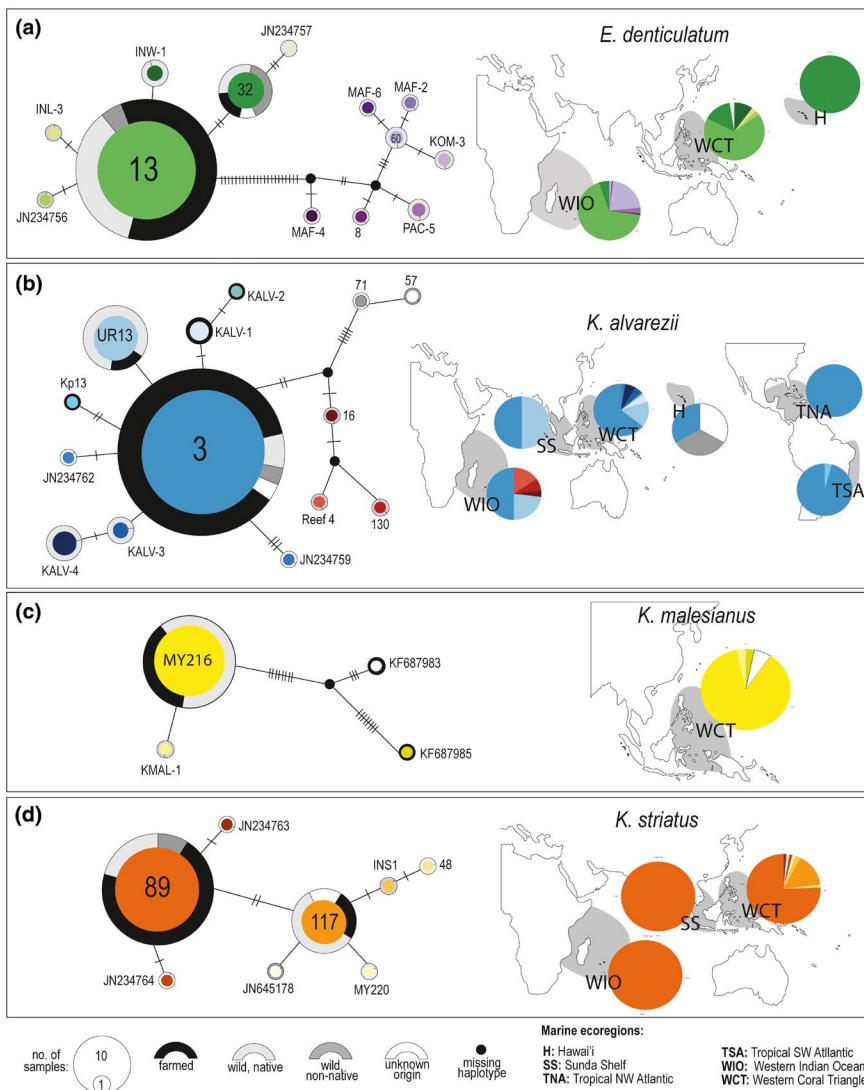


FIGURE 2 Haplotype networks and the geographic distribution of haplotypes of the four cultivated eucheumatoid species *Eucheuma denticulatum* (a), *Kappaphycus alvarezii* (b), *K. striatus* (c), *K. malesianus* (d), using the mitochondrial genetic sequence *cox2-3 spacer* as a marker. In the haplotype network, the size of the nodes relates to the number of sequences in Genbank, the colour of the inner circle relates to the geographic origin, the colour of the outer circle indicates the specimen origin (farmed, wild native, wild non-native). For the geographic distribution specimen were grouped according to their sampling location in marine ecoregions (following Spalding et al., 2007). Note that this does not necessarily reflect the indigenous diversity, as molecular information is biased towards farmed specimens and includes introduced specimens (see Figure 1 for major introduction events)

ACKNOWLEDGEMENTS

CMMG, JaB, RCS, PEL, IC, EJCC, VM, GW, VLM, FEM, JuB were supported by the United Kingdom Research and Innovation–Global Challenges Research Fund (UKRI- GCRF) ‘GlobalSeaweedSTAR’ Programme (Grant No. BB/P027806/1), which also supported RVD

through the research fund GSS/RF/015. RVD would like to thank the Department of Science and Technology (DOST), Philippine Council for Agriculture, Aquatic and Natural Resources Research and Development (PCAARRD) under the program, Establishment of Seaweed Research and Development Center (SeaRDeC) to Support

the Seaweed Industry in BARMM, Project 2: Molecular characterization, selection and production of high quality euchematoid cultivars in the Bangsamoro Autonomous Region in Muslim Mindanao. We also thank the interdisciplinary discussions and comments from the GlobalSeaweedSTAR team, specifically Jee Suyu, Ivy Matoju, Azam Asri, Adibi M. Nor and Louise Shaxson.

AUTHORS' CONTRIBUTION

CMMG conceptualised the manuscript, CMMG and JaB and wrote the main text body of the review, RCS, JaB and CMMG wrote the case study, RVD, JaB and CMMG analysed data and developed figures for the review, LT and PEL provided data for the review, VM provided data and text for the review, RVD, IC, EJCC, GW, VLM, FEM, JuB, PEL edited the review and provided their expertise.

ORCID

Richard V. Dumilag <http://orcid.org/0000-0002-7590-0009>

Flower E. Msuya  <https://orcid.org/0000-0001-6578-6268>

Juliet Brodie  <https://orcid.org/0000-0001-7622-2564>

Claire M. M. Gachon  <https://orcid.org/0000-0002-3702-7472>

REFERENCES

- Ahmadi, N., Bertrand, B., & Glaszmann, J.-C. (2013). Rethinking plant breeding. In E. Hainzlin (Ed.), *Cultivating biodiversity to transform agriculture* (pp. 91–140). Springer.
- Alibon, R. D., Gonzales, J. M. P., Ordoño, A. E. T., & Echem, R. T. (2019). Incidence of ice-ice disease associated with *Kappaphycus alvarezii* in the seaweed farms in Zamboanga Peninsula, Mindanao, Philippines. *SSR Institute of International Journal of Life Sciences*, 5(1), 2148–2155. <https://doi.org/10.21276/SSR-IJLS.2019.5.1.6>
- Arafeh-Dalmau, N., Schoeman, D. S., Montaña-Moctezuma, G., Micheli, F., Rogers-Bennett, L., Olguin-Jacobson, C., & Possingham, H. P. (2020). Marine heat waves threaten kelp forests. *Science*, 367(6478), 635. <https://doi.org/10.1126/science.aba5244>
- Araújo, P. G., Nardelli, A. E., Gelli, V. C., Fujii, M. T., & Chow, F. (2020). Monitoring environmental risk of the exotic species *Kappaphycus alvarezii* (Rhodophyta), after two decades of introduction in southeastern Brazil. *Botanica Marina*, 63(6), 551–558. <https://doi.org/10.1515/bot-2020-0052>
- Araújo, P. G., Schmidt, É. C., Kreuzsch, M. G., Kano, C. H., Guimarães, S. M. P. B., Bouzon, Z. L., Fujii, M. T., & Yokoya, N. S. (2014). Ultrastructural, morphological, and molecular characterization of *Colaconema infestans* (Colaconematales, Rhodophyta) and its host *Kappaphycus alvarezii* (Gigartinales, Rhodophyta) cultivated in the Brazilian tropical region. *Journal of Applied Phycology*, 26(5), 1953–1961. <https://doi.org/10.1007/s10811-014-0348-9>
- Arnaud-Haond, S., Arrieta, J. M., & Duarte, C. M. (2011). Marine biodiversity and gene patents. *Science*, 331(6024), 1521–1522. <https://doi.org/10.1126/science.1200783>
- Arrieta, J. M., Arnaud-Haond, S., & Duarte, C. M. (2010). What lies underneath: Conserving the oceans' genetic resources. *Proceedings of the National Academy of Sciences*, 107(43), 18318–18324. <https://doi.org/10.1073/PNAS.0911897107>
- Ask, E., Batibasaga, A., Zertuche-González, J. A., & de San, M. (2003). Three decades of *Kappaphycus alvarezii* (Rhodophyta) introduction to non-endemic locations. *International Seaweed Symposium*, 17, 49–57.
- Azizi, A., Mohd Hanafi, N., Basiran, M. N., & Teo, C. H. (2018). Evaluation of disease resistance and tolerance to elevated temperature stress of the selected tissue-cultured *Kappaphycus alvarezii* Doty 1985 under optimized laboratory conditions. *3 Biotech*, 8(8), 321. <https://doi.org/10.1007/s13205-018-1354-4>
- Badis, Y., Klochkova, T. A., Brakel, J., Arce, P., Tringe, S. G., Kim, G. H., & Gachon, C. M. M. (2019). Hidden diversity in the oomycete genus *Olpidiopsis* is a potential hazard to red algal cultivation and conservation worldwide. *European Journal of Phycology*, 00(00), 1–10. <https://doi.org/10.1080/09670262.2019.1664769>
- Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, 12(4), <https://doi.org/10.1098/rsbl.2015.0623>
- Bjerregaard, R., Valderrama, D., Radulovich, R., Diana, J., Capron, M., Mckinnie, C. A., Cedric, M., Hopkins, K., Yarish, C., & Goudey, C. (2016). *Seaweed aquaculture for food security, income generation and environmental health in tropical developing countries*. The World Bank. <https://doi.org/10.1596/24919>
- Blasiak, R., Jouffray, J. B., Wabnitz, C. C. C., Sundström, E., & Osterblom, H. (2018). Corporate control and global governance of marine genetic resources. *Science Advances*, 4(6), eaar5237. <https://doi.org/10.1126/sciadv.aar5237>
- Brodie, J., Pottas, J., & Wilbraham, J. (2014). Draft Red Data list of UK seaweeds. <https://www.nhm.ac.uk/content/dam/nhmwww/our-science/our-work/biodiversity/draft-seaweed-list.pdf>
- Brodie, J., Williamson, C. J., Smale, D. A., Kamenos, N. A., Mieszkowska, N., Santos, R., Cunliffe, M., Steinke, M., Yesson, C., Anderson, K. M., Asnaghi, V., Brownlee, C., Burdett, H. L., Burrows, M. T., Collins, S., Donohue, P. J. C., Harvey, B., Foggo, A., Noisette, F., ... Hall-Spencer, J. M. (2014). The future of the northeast Atlantic benthic flora in a high CO2 world. *Ecology and Evolution*, 4(13), 2787–2798. <https://doi.org/10.1002/ece3.1105>
- Bustamante, D. E., Won, B. Y., & Cho, T. O. (2015). First record of *Neosiphonia echinata* (Rhodomelaceae, Rhodophyta) in the South Pacific: An introduced species in Southeast Asia. *Botanica Marina*, 58(5), 345–354. <https://doi.org/10.1515/bot-2015-0015>
- Cabrera Medaglia, J., Oguamanam, C., Rukundo, O., & Perron-Welch, F. (2019). Comparative study of the nagoya protocol, the plant treaty and the UPOV convention: The interface of access and benefit sharing and plant variety protection. *SSRN Electronic Journal*, 1–48. <https://doi.org/10.2139/ssrn.3393475>
- Campbell, I., Kambey, C. S. B., Mateo, J. P., Rusekwa, S. B., Hurtado, A. Q., Msuya, F. E., Stentiford, G. D., & Cottier-Cook, E. J. (2019). Biosecurity policy and legislation for the global seaweed aquaculture industry. *Journal of Applied Phycology*, <https://doi.org/10.1007/s10811-019-02010-5>
- Cleves, P. A., Shumaker, A., Lee, J. M., Putnam, H. M., & Bhattacharya, D. (2020). Unknown to known: Advancing knowledge of coral gene function. *Trends in Genetics*, 36(2), 93–104. <https://doi.org/10.1016/j.tig.2019.11.001>
- Cock, J. M., Godfroy, O., Macaisne, N., Peters, A. F., & Coelho, S. M. (2014). Evolution and regulation of complex life cycles: A brown algal perspective. *Current Opinion in Plant Biology*, 17(1), 1–6. <https://doi.org/10.1016/j.pbi.2013.09.004>
- Coleman, M. A., & Goold, H. D. (2019). Harnessing synthetic biology for kelp forest conservation. *Journal of Phycology*, 55(4), 745–751. <https://doi.org/10.1111/jpy.12888>
- Costello, M. J., & Chaudhary, C. (2017). Marine biodiversity, biogeography, deep-sea gradients, and conservation. *Current Biology*, 27(11), R511–R527. <https://doi.org/10.1016/j.cub.2017.04.060>
- Cottier-Cook, E. J., Nagabhatla, N., Badis, Y., Campbell, M., Chopin, T., Dai, W., Fang, J., He, P., Hewitt, C., & Kim, G. H. (2016). Safeguarding the future of the global seaweed aquaculture industry. United Nations University and Scottish Association for Marine Science. Policy Brief. 12pp. <https://www.sams.ac.uk/t4-media/sams/pdf/globalseaweed-policy-brief.pdf>

- de Vargas, C., Audic, S., Henry, N., Decelle, J., Mahé, F., Logares, R., Lara, E., Berney, C., Le Bescot, N., Probert, I., Carmichael, M., Poulain, J., Romac, S., Colin, S., Aury, J.-M., Bittner, L., Chaffron, S., Dunthorn, M., Engelen, S., ... Karsenti, E. (2015). Eukaryotic plankton diversity in the sunlit ocean. *Science*, 348(6237), 1261605–1/11. <https://doi.org/10.1007/s13398-014-0173-7.2>
- Dittami, S. M., Corre, E., Brillet-Guéguen, L., Lipinska, A. P., Pontoizeau, N., Aite, M., Avia, K., Caron, C., Cho, C. H., Collén, J., Cormier, A., Delage, L., Doubleau, S., Frioux, C., Gobet, A., González-Navarrete, I., Groisillier, A., Hervé, C., Jollivet, D., ... Tonon, T. (2020). The genome of *Ectocarpus subulatus* – A highly stress-tolerant brown alga. *Marine Genomics*, 52, 100740. <https://doi.org/10.1016/j.margen.2020.100740>
- Diz, D. (2018). Marine biodiversity: Opportunities for global governance and management coherence. In M. Salomon, & T. Markus (Eds.), *Handbook on marine environment protection: Science, impacts and sustainable management* (pp. 855–870). Springer International Publishing. https://doi.org/10.1007/978-3-319-60156-4_45
- Duarte, C. M., Marbá, N., & Holmer, M. (2007). Rapid domestication of marine species. *Science*, 316(5823), 382–383. <https://doi.org/10.1126/science.1138042>
- Dumilag, R. V., Orosco, F. L., & Lluisma, A. O. (2016). Genetic diversity of *Kappaphycus* species (Gigartinales, Rhodophyta) in the Philippines. *Systematics and Biodiversity*, 14(5), 441–451. <https://doi.org/10.1080/14772000.2016.1157643>
- Dumilag, R. V., Salvador, R. C., & Halling, C. (2016). Genotype introduction affects population composition of native Philippine *Kappaphycus* (Gigartinales, Rhodophyta). *Conservation Genetics Resources*, 8(4), 439–441. <https://doi.org/10.1007/s12686-016-0591-2>
- Eggertsen, M., & Halling, C. (2020). Knowledge gaps and management recommendations for future paths of sustainable seaweed farming in the Western Indian Ocean. *Ambio*, 50(1), 60–73. <https://doi.org/10.1007/s13280-020-01319-7>
- Fabricius, K. E., Kluibenschedl, A., Harrington, L., Noonan, S., & De'ath, G. (2015). In situ changes of tropical crustose coralline algae along carbon dioxide gradients. *Scientific Reports*, 5, 1–7. <https://doi.org/10.1038/srep09537>
- FAO (2019). The State of the World's Aquatic Genetic Resources for Food and Agriculture. <http://www.fao.org/3/CA5256EN/CA5256EN.pdf>
- FAO (2020). The State of the World Fisheries and Aquaculture 2020. Sustainability in action. <https://doi.org/10.4060/ca9229en>
- Fleurence, J. (2004). Seaweed proteins. In R. Y. Yada (Ed.), *Proteins in food processing (Issue April 2004)* (pp. 197–213). Woodhead Publishing. <https://doi.org/10.1533/9781855738379.1.197>
- Ganzon-Fortes, E. T., Trono, G. C., Villanueva, R. D., Romero, J. B., & Montaña, M. N. E. (2012). “Endong”, a rare variety of the farmed carrageenophyte *Eucheuma denticulatum* (Burman) Collins & Hervey from the Philippines. *Journal of Applied Phycology*, 24(5), 1107–1111. <https://doi.org/10.1007/s10811-011-9740-x>
- Goecke, F., Klemetsdal, G., & Ergon, Å. (2020). Cultivar development of kelps for commercial cultivation—Past lessons and future prospects. *Frontiers in Marine Science*, 8(February), 110. <https://doi.org/10.3389/fmars.2020.00110>
- Grulois, D., Lévêque, L., & Viard, F. (2011). Mosaic genetic structure and sustainable establishment of the invasive kelp *Undaria pinnatifida* within a bay (Bay of St-Malo, Brittany). *Cahiers De Biologie Marine*, 52(4), 485–498.
- Guillemain, M.-L., Faugeton, S., Destombe, C., Viard, F., Correa, J. A., & Valero, M. (2008). Genetic variation in wild and cultivated populations of the haploid-diploid red alga *Gracilaria chilensis*: How farming practices favor asexual reproduction and heterozygosity. *Evolution*, 62(6), 1500–1519. <https://doi.org/10.1111/j.1558-5646.2008.00373.x>
- Guillemain, M.-L., Valero, M., Faugeton, S., Nelson, W., & Destombe, C. (2014). Tracing the trans-pacific evolutionary history of a domesticated seaweed (*Gracilaria chilensis*) with archaeological and genetic data. *PLoS One*, 9(12), 1–17. <https://doi.org/10.1371/journal.pone.0114039>
- Guzinski, J., Ballenghien, M., Daguin-Thiébaud, C., Lévêque, L., & Viard, F. (2018). Population genomics of the introduced and cultivated Pacific kelp *Undaria pinnatifida*: Marinas—not farms—drive regional connectivity and establishment in natural rocky reefs. *Evolutionary Applications*, 11(9), 1582–1597. <https://doi.org/10.1111/eva.12647>
- Guzinski, J., Mauger, S., Cock, J. M., & Valero, M. (2016). Characterization of newly developed expressed sequence tag-derived microsatellite markers revealed low genetic diversity within and low connectivity between European *Saccharina latissima* populations. *Journal of Applied Phycology*, 28(5), 3057–3070. <https://doi.org/10.1007/s10811-016-0806-7>
- Hainzelin, É. (2013). *Cultivating biodiversity to transform agriculture (Issue BOOK)*. Springer.
- Halling, C., Wikström, S. A., Lilliesköld-Sjöö, G., Mörk, E., Lundsør, E., & Zuccarello, G. C. (2013). Introduction of Asian strains and low genetic variation in farmed seaweeds: Indications for new management practices. *Journal of Applied Phycology*, 25(1), 89–95. <https://doi.org/10.1007/s10811-012-9842-0>
- Hickey, J. M., Chiurugwi, T., Mackay, I., & Powell, W. (2017). Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery. *Nature Genetics*, 49(9), 1297–1303. <https://doi.org/10.1038/ng.3920>
- Holdt, S. L., & Kraan, S. (2011). Bioactive compounds in seaweed: Functional food applications and legislation. *Journal of Applied Phycology*, 23(3), 543–597. <https://doi.org/10.1007/s10811-010-9632-5>
- Hu, Z. M., Duan, D.-L., & Lopez-Bautista, J. (2016). Seaweed phylogeography from 1994 to 2014: An overview. In Z.-M. Hu & C. Fraser (Eds.), *Seaweed phylogeography* (pp. 3–22). Springer. <https://doi.org/10.1007/978-94-017-7534-2>
- Hurtado, A. Q., Critchley, A. T., Trespoey, A., & Lhonneur, G. B. (2006). Occurrence of *Polysiphonia* epiphytes in *Kappaphycus* farms at Calaguas Is., Camarines Norte, Philippines. *Journal of Applied Phycology*, 18(3–5), 301–306. <https://doi.org/10.1007/s10811-006-9032-z>
- Hurtado, A. Q., Gerung, G. S., Yasir, S., & Critchley, A. T. (2014). Cultivation of tropical red seaweeds in the BIMP-EAGA region. *Journal of Applied Phycology*, 26(2), 707–718. <https://doi.org/10.1007/s10811-013-0116-2>
- Hurtado, A. Q., Lim, P. E., Tan, J., Phang, S. M., Neish, I. C., & Critchley, A. T. (2016). Biodiversity and biogeography of commercial tropical carrageenophytes in the southeast asian region. In A. Q. Hurtado, A. T. Critchley, & I. C. Neish (Eds.), *Carrageenans: Sources and extraction methods, molecular structure, bioactive properties and health effects* (pp. 51–74). Springer International Publishing AG.
- Hwang, E. K., Yotsukura, N., Pang, S. J., Su, L., & Shan, T. F. (2019). Seaweed breeding programs and progress in eastern Asian countries. *Phycologia*, 58(5), 484–495. <https://doi.org/10.1080/0031884.2019.1639436>
- Ichihara, K., Yamazaki, T., Miyamura, S., Hiraoka, M., & Kawano, S. (2019). Asexual thalli originated from sporophytic thalli via apomeiosis in the green seaweed *Ulva*. *Scientific Reports*, 9(1), 1–12. <https://doi.org/10.1038/s41598-019-50070-x>
- Kambey, C. S. B., Campbell, I., Sondak, C. F. A., Nor, A. R. M., Lim, P. E., & Cottier-Cook, E. J. (2020). An analysis of the current status and future of biosecurity frameworks for the Indonesian seaweed industry. *Journal of Applied Phycology*, 32(4), 2147–2160. <https://doi.org/10.1007/s10811-019-02020-3>
- Kelly, E. L. A., Cannon, A. L., & Smith, J. E. (2020). Environmental impacts and implications of tropical carrageenophyte seaweed farming. *Conservation Biology*, 34(2), 326–337. <https://doi.org/10.1111/cobi.13462>

- Krueger-Hadfield, S. A. (2020). What's ploidy got to do with it? Understanding the evolutionary ecology of macroalgal invasions necessitates incorporating life cycle complexity. *Evolutionary Applications*, 13(3), 486–499. <https://doi.org/10.1111/eva.12843>
- Kumar, M., Kuzhiumparambil, U., Pernice, M., Jiang, Z., & Ralph, P. J. (2016). Metabolics: An emerging frontier of systems biology in marine macrophytes. *Algal Research*, 16, 76–92. <https://doi.org/10.1016/j.algal.2016.02.033>
- Kumar, Y. N., Poong, S., Gachon, C., Brodie, J., Sade, A., & Id, P. L. (2020). Impact of elevated temperature on the physiological and biochemical responses of *Kappaphycus alvarezii* (Rhodophyta). *PLoS One*, 15(9), e0239097. <https://doi.org/10.1371/journal.pone.0239097>
- Laike, L., Hoban, S., Bruford, M. W., Segelbacher, G., Allendorf, F. W., Gajardo, G., Rodríguez, A. G., Hedrick, P. W., Heuertz, M., Hohenlohe, P. A., Jaffé, R., Johannesson, K., Liggins, L., MacDonald, A. J., OrozcoaterWengel, P., Reusch, T. B. H., Rodríguez-Correa, H., Russo, I.-R.-M., Ryman, N., & Vernesi, C. (2020). Post-2020 goals overlook genetic diversity. *Science*, 367(6482), 2–5. <https://doi.org/10.1126/science.abb2748>
- Largo, D. B. (2002). Recent developments in seaweed diseases. Proceedings of the National Seaweed Planning Workshop Held on August 2-3, 2001, 35–42. <https://repository.seafdec.org.ph/bitstream/handle/10862/196/9718511571p35-42.pdf;jsessionid=6F59AF8761CBACAE4516B038D0050D36.jvm1?sequence=1>
- Largo, D. B., Fukami, K., & Nishijima, T. (1995). Occasional pathogenic bacteria promoting ice-ice disease in the carrageenan-producing red algae *Kappaphycus alvarezii* and *Eucheuma denticulatum* (Solieriaceae, Gigartinales, Rhodophyta). *Journal of Applied Phycology*, 7(6), 545–554. <https://doi.org/10.1007/BF00003941>
- Largo, D. B., Fukami, K., Nishijima, T., & Ohno, M. (1995). Laboratory-induced development of the ice-ice disease of the farmed red algae *Kappaphycus alvarezii* and *Eucheuma denticulatum* (Solieriaceae, Gigartinales, Rhodophyta). *Journal of Applied Phycology*, 7(6), 539–543. <https://doi.org/10.1007/BF00003940>
- Largo, D. B., Msuya, F. E., & Menezes, A. (2020). Understanding diseases and control in seaweed farming in Zanzibar. In *FAO Fisheries and Aquaculture Technical Paper No. 662*. (pp. 1–64). FAO. <https://doi.org/10.4060/ca9004en>
- Le Cam, S., Daguin-Thiébaud, C., Bouchemousse, S., Engelen, A. H., Mieszowska, N., & Viard, F. (2019). A genome-wide investigation of the worldwide invader *Sargassum muticum* shows high success albeit (almost) no genetic diversity. *Evolutionary Applications*, April 2019, 500–514. <https://doi.org/10.1111/eva.12837>
- Li, J., Pang, S., & Shan, T. (2017). Existence of an intact male life cycle offers a novel way in pure-line crossbreeding in the brown alga *Undaria pinnatifida*. *Journal of Applied Phycology*, 29(2), 993–999. <https://doi.org/10.1007/s10811-016-1005-2>
- Lim, P. E., Yang, L. E., Tan, J., Maggs, C. A., & Brodie, J. A. (2017). Advancing the taxonomy of economically important red seaweeds (Rhodophyta). *European Journal of Phycology*, 52(4), 438–451. <https://doi.org/10.1080/09670262.2017.1365174>
- Lipinska, A. P., Ahmed, S., Peters, A. F., Faugeton, S., Cock, J. M., & Coelho, S. M. (2015). Development of PCR-based markers to determine the sex of kelps. *PLoS One*, 10(10), 1–15. <https://doi.org/10.1371/journal.pone.0140535>
- Loureiro, R., Gachon, C. M. M., & Rebours, C. (2015). Seaweed cultivation: Potential and challenges of crop domestication at an unprecedented pace. *New Phytologist*, 206(2), 489–492. <https://doi.org/10.1111/nph.13278>
- Luhan, M. R. J., & Mateo, J. P. (2017). Clonal production of *Kappaphycus alvarezii* (Doty) Doty in vitro. *Journal of Applied Phycology*, 29(5), 2339–2344. <https://doi.org/10.1007/s10811-017-1105-7>
- Luhan, M. R. J., & Sollesta, H. (2010). Growing the reproductive cells (carpospores) of the seaweed, *Kappaphycus striatum*, in the laboratory until outplanting in the field and maturation to tetrasporophyte. *Journal of Applied Phycology*, 22(5), 579–585. <https://doi.org/10.1007/s10811-009-9497-7>
- Maggs, C. A. (1988). Intraspecific life history variability in the florideophycidae (Rhodophyta). *Botanica Marina*, 31(6), 465–490. <https://doi.org/10.1515/botm.1988.31.6.465>
- Martino, J. V., Van Limbergen, J., & Cahill, L. E. (2017). The role of carrageenan and carboxymethylcellulose in the development of intestinal inflammation. *Frontiers in Pediatrics*, 5(May), 1–7. <https://doi.org/10.3389/fped.2017.00096>
- Mateo, J. P., Campbell, I., Cottier-Cook, E. J., Luhan, M. R. J., Ferriols, V. M. E. N., & Hurtado, A. Q. (2020). Analysis of biosecurity-related policies governing the seaweed industry of the Philippines. *Journal of Applied Phycology*, 32(3), 2009–2022. <https://doi.org/10.1007/s10811-020-02083-7>
- Mazarrasa, I., Olsen, Y. S., Mayol, E., Marbà, N., & Duarte, C. M. (2013). Rapid growth of seaweed biotechnology provides opportunities for developing nations. *Nature Biotechnology*, 31(7), 591–592. <https://doi.org/10.1038/nbt.2636>
- Mignerot, L., Avia, K., Luthringer, R., Lipinska, A. P., Peters, A. F., Cock, J. M., & Coelho, S. M. (2019). A key role for sex chromosomes in the regulation of parthenogenesis in the brown alga *Ectocarpus*. *PLoS Genetics*, 15(6), 1–25. <https://doi.org/10.1371/journal.pgen.1008211>
- Mineur, F., Le Roux, A., Maggs, C. A., & Verlaque, M. (2014). Positive feedback loop between introductions of non-native marine species and cultivation of oysters in Europe. *Conservation Biology*, 28(6), 1667–1676. <https://doi.org/10.1111/cobi.12363>
- Montes, H. R. Jr, Pobre, K. F. R., & Lluisma, A. O. (2008). Phylogenetic affiliation of the "Endong"/"Spaghetti" variety of *Eucheuma* as revealed by molecular data. *Philippine Agricultural Scientist*, 91(1), 86–93.
- Mshigeni, K. E. (1984). The red algal genus *Eucheuma* (Gigartinales, Solieriaceae) in East Africa: An underexploited resource. *Hydrobiologia*, 116–117(1), 347–350. <https://doi.org/10.1007/BF00027700>
- Msuya, F. E. (2006). The impact of seaweed farming on the social and economic structure of seaweed farming communities in Zanzibar, Tanzania. In A. T. Critchley, M. Ohno, & D. B. Largo (Eds.), *World seaweed resources: An authoritative reference system* (Vol. 1, pp. 2–27). ETI Bioinformatics.
- Msuya, F. E., Buriyo, A., Omar, I., Pascal, B., Narrain, K., Ravina, J. J. M., Mrabu, E., & Wakibia, J. G. (2014). Cultivation and utilisation of red seaweeds in the Western Indian Ocean (WIO) Region. *Journal of Applied Phycology*, 26(2), 699–705. <https://doi.org/10.1007/s10811-013-0086-4>
- Msuya, F. E., & Hurtado, A. Q. (2017). The role of women in seaweed aquaculture in the Western Indian Ocean and South-East Asia. *European Journal of Phycology*, 52(4), 482–494. <https://doi.org/10.1080/09670262.2017.1357084>
- Msuya, F. E., & Porter, M. (2014). Impact of environmental changes on farmed seaweed and farmers: The case of Songo Songo Island, Tanzania. *Journal of Applied Phycology*, 26(5), 2135–2141. <https://doi.org/10.1007/s10811-014-0243-4>
- Neori, A., Chopin, T., Troell, M., Buschmann, A. H., Kraemer, G. P., Halling, C., Shpigel, M., & Yarish, C. (2004). Integrated aquaculture: Rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. *Aquaculture*, 231(1–4), 361–391. <https://doi.org/10.1016/j.aquaculture.2003.11.015>
- Nimmo, A. H. (1986). Recent population movements in the Sulu Archipelago: Implications to Sama culture history. *Archipel*, 32(1), 25–38. <https://doi.org/10.3406/arch.1986.2307>
- Nor, A. M., Gray, T. S., Caldwell, G. S., & Stead, S. M. (2017). Is a cooperative approach to seaweed farming effectual? An analysis of the seaweed cluster project (SCP), Malaysia. *Journal of Applied Phycology*, 29(5), 2323–2337. <https://doi.org/10.1007/s10811-016-1025-y>
- Quiaioit, H. A. R., Uy, W. H., Bacaltos, D. G. G., & Chio, P. B. R. (2016). In A. C. T. Acenas (Ed.), *Seaweed area GIS-based mapping. Production*

- support system for sustainable seaweed farming in the Philippines 2016 report. Xavier University Press. <http://www.xu.edu.ph/xu-press>
- Rebours, C., Marinho-Soriano, E., Zertuche-González, J. A., Hayashi, L., Vásquez, J. A., Kradolfer, P., Soriano, G., Ugarte, R., Abreu, M. H., Bay-Larsen, I., Hovelsrud, G., Rødven, R., & Robledo, D. (2014). Seaweeds: An opportunity for wealth and sustainable livelihood for coastal communities. *Journal of Applied Phycology*, 26(5), 1939–1951. <https://doi.org/10.1007/s10811-014-0304-8>
- Rusekwa, S. B., Campbell, I., Msuya, F. E., Buriyo, A. S., & Cottier-Cook, E. J. (2020). Biosecurity policy and legislation of the seaweed aquaculture industry in Tanzania. *Journal of Applied Phycology*, <https://doi.org/10.1007/s10811-020-02194-1>
- Sade, A., Ali, I., & Ariff, M. R. M. (2006). The seaweed industry in Sabah, east Malaysia. *Jati-Journal of Southeast Asian Studies*, 11, 97–107.
- Sellers, A. J., Saltonstall, K., & Davidson, T. M. (2015). The introduced alga *Kappaphycus alvarezii* (Doty ex P.C. Silva, 1996) in abandoned cultivation sites in Bocas del Toro, Panama. *BioInvasions Records*, 4(1), 1–7. <https://doi.org/10.3391/bir.2015.4.1.01>
- Shan, T., Pang, S., Li, J., Li, X., & Su, L. (2015). Construction of a high-density genetic map and mapping of a sex-linked locus for the brown alga *Undaria pinnatifida* (Phaeophyceae) based on large scale marker development by specific length amplified fragment (SLAF) sequencing. *BMC Genomics*, 16(1), 1–10. <https://doi.org/10.1186/s12864-015-2184-y>
- Shan, T., Pang, S., Wang, X., Li, J., & Su, L. (2018). Assessment of the genetic connectivity between farmed and wild populations of *Undaria pinnatifida* (Phaeophyceae) in a representative traditional farming region of China by using newly developed microsatellite markers. *Journal of Applied Phycology*, 30(4), 2707–2714. <https://doi.org/10.1007/s10811-018-1449-7>
- Smale, D. A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytologist*, 225(4), 1447–1454. <https://doi.org/10.1111/nph.16107>
- Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdeña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, 57(7), 573–583. <https://doi.org/10.1641/B570707>
- Stat, M., Huggett, M. J., Bernasconi, R., Dibattista, J. D., Berry, T. E., Newman, S. J., Harvey, E. S., & Bunce, M. (2017). Ecosystem biomonitoring with eDNA: Metabarcoding across the tree of life in a tropical marine environment. *Scientific Reports*, 7(1), 1–11. <https://doi.org/10.1038/s41598-017-12501-5>
- Stentiford, G. D., Neil, D., Peeler, E., Shields, J., Small, H., Flegel, T., Vlask, J., Jones, B., Morado, F., Moss, S., Bartholomay, L., Behringer, D., Hauton, C., & Lightner, D. (2012). Disease will limit future food supply from the global crustacean fishery. *Journal of Invertebrate Pathology*, 110, 141–157. <https://doi.org/10.1016/j.jip.2012.03.013>
- Takahashi, M., & Mikami, K. (2017). Oxidative stress promotes asexual reproduction and apogamy in the red seaweed *Pyropia yezoensis*. *Frontiers in Plant Science*, 8(JANUARY), 1–6. <https://doi.org/10.3389/fpls.2017.00062>
- Tan, J., Lim, P. E., & Phang, S. M. (2013). Phylogenetic relationship of *Kappaphycus* Doty and *Eucheuma* J. Agardh (Solieriaceae, Rhodophyta) in Malaysia. *Journal of Applied Phycology*, 25(1), 13–29. <https://doi.org/10.1007/s10811-012-9833-1>
- Tanksley, S. D., & McCouch, S. R. (1997). Seed banks and molecular maps: Unlocking genetic potential from the wild. *Science*, 277(5329), 1063–1066. <https://doi.org/10.1126/science.277.5329.1063>
- Tano, S. A., Halling, C., Lind, E., Buriyo, A., & Wikström, S. A. (2015). Extensive spread of farmed seaweeds causes a shift from native to non-native haplotypes in natural seaweed beds. *Marine Biology*, 162(10), 1983–1992. <https://doi.org/10.1007/s00227-015-2724-7>
- Tisera, W. L., & Naguit, M. R. A. (2009). Ice-ice disease occurrence in seaweed farms in Bais Bay, Negros Oriental and Zamboanga del Norte. *The Threshold*, 4, 1–16.
- Torres, P., Santos, J. P., Chow, F., & dos Santos, D. Y. A. C. (2019). A comprehensive review of traditional uses, bioactivity potential, and chemical diversity of the genus *Gracilaria* (Gracilariaceae, Rhodophyta). *Algal Research*, 37, 288–306. <https://doi.org/10.1016/j.algal.2018.12.009>
- Trono, G. C. (1999). Diversity of the seaweed flora of the Philippines and its utilization. *Hydrobiologia*, 398(399), 1–6.
- Tsiresy, G., Preux, J., Lavitra, T., Dubois, P., Lepoint, G., & Eeckhaut, I. (2016). Phenology of farmed seaweed *Kappaphycus alvarezii* infestation by the parasitic epiphyte *Polysiphonia* sp. in Madagascar. *Journal of Applied Phycology*, 2903–2914. <https://doi.org/10.1007/s10811-016-0813-8>
- Umen, J., & Coelho, S. (2019). Algal sex determination and the evolution of anisogamy. *Annual Review of Microbiology*, 73(1), 267–291. <https://doi.org/10.1146/annurev-micro-020518-120011>
- Vairappan, C. S., Chung, C. S., Hurtado, A. Q., Soya, F. E., Lhonneur, G. B., & Critchley, A. (2008). Distribution and symptoms of epiphyte infection in major carrageenophyte-producing farms. *Journal of Applied Phycology*, 20, 477–483. <https://doi.org/10.1007/s10811-007-9299-8>
- Valero, M., Guillemain, M., Destombe, C., Jacquemin, B., Gachon, C. M. M., Badis, Y., Buschmann, A. H., Camus, C., & Faugeton, S. (2017). Perspectives on domestication research for sustainable seaweed aquaculture. *Perspectives in Phycology*, 4(1), 33–46. <https://doi.org/10.1127/pip/2017/0066>
- Vanagt, T., Broggiato, A., Lallier, L. E., Jaspars, M., Burton, G., & Muyldermans, D. (2019). Conserving Biodiversity in Areas beyond National Jurisdiction. In D. Freestone (Ed.), *Mare geneticum: Towards an implementing agreement for marine genetic resources in international waters* (pp. 267–297). Brill. https://doi.org/10.1163/9789004391703_012
- Varela-Álvarez, E., Loureiro, J., Paulino, C., & Serrão, E. A. (2018). Polyploid lineages in the genus *Porphyra*. *Scientific Reports*, 8(1), 1–15. <https://doi.org/10.1038/s41598-018-26796-5>
- Vierros, M., Suttle, C. A., Harden-Davies, H., & Burton, G. (2016). Who Owns the Ocean? Policy Issues Surrounding Marine Genetic Resources Ocean diversity and the potential for bio-discovery. Association for the Sciences Limnology and Oceanography. May, 2–8.
- Wade, R., Augyte, S., Harden, M., Nuzhdin, S., Yarish, C., & Alberto, F. (2020). Macroalgal germplasm banking for conservation, food security, and industry. *PLoS Biology*, 18(2), 1–10. <https://doi.org/10.1371/journal.pbio.3000641>
- Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C. J., Hovey, R. K., Harvey, E. S., Holmes, T. H., Kendrick, G. A., Radford, B., Santanagarçon, J., Saunders, B. J., Smale, D. A., Thomsen, M. S., Tuckett, C. A., ... Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, 353(6295), 169–172. <https://doi.org/10.1126/science.aad8745>
- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J., & Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314(5800), 787–790. <https://doi.org/10.1126/science.1132294>
- Yang, L.-E., Deng, Y.-Y., Xu, G.-P., Russell, S., Lu, Q.-Q., & Brodie, J. A. (2020). Redefining *Pyropia* (Bangiales, Rhodophyta): Four new genera, resurrection of *Porphyrella* and description of *Calidia pseudobolobata* sp. nov. from China. *Journal of Phycology*, 44, <https://doi.org/10.1111/jpy.12992>
- Zhang, J., Wang, X., Yao, J., Li, Q., Liu, F., Yotsukura, N., Krupnova, T. N., & Duan, D. (2017). Effect of domestication on the genetic diversity

- and structure of *Saccharina japonica* populations in China. *Scientific Reports*, 7(January), 1–11. <https://doi.org/10.1038/srep42158>
- Zhang, N., Zhang, L., Tao, Y., Guo, L., Sun, J., Li, X., Zhao, N., Peng, J., Li, X., Zeng, L., Chen, J., & Yang, G. (2015). Construction of a high density SNP linkage map of kelp (*Saccharina japonica*) by sequencing Taq I site associated DNA and mapping of a sex determining locus. *BMC Genomics*, 16(1), 1–11. <https://doi.org/10.1186/s12864-015-1371-1>
- Zuccarello, G. C., Critchley, A. T., Smith, J., Sieber, V., Lhonneur, G. B., & West, J. A. (2006). Systematics and genetic variation in commercial shape *Kappaphycus* and shape *Euचेuma* (Solieriaceae, Rhodophyta). *Journal of Applied Phycology*, 18(3–5), 643–651. <https://doi.org/10.1007/s10811-006-9066-2>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Brakel J, Sibonga RC, Dumilag RV, et al. Exploring, harnessing and conserving marine genetic resources towards a sustainable seaweed aquaculture. *Plants, People, Planet*. 2021;3:337–349. <https://doi.org/10.1002/ppp3.10190>