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REVIEW



The Diversity of Eucheumatoid Seaweed Cultivars in the Philippines

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ABSTRACT

Collectively known as eucheumatoids, *Eucheuma denticulatum*, *Kappaphycus alvarezii*, *K. malesianus*, and *K. striatus* are the main farmed seaweed species in the Philippines. The success of seaweed farming for over five decades in the country is due, in part, to the high diversity of cultivars maintained by the Filipino farmers. Notwithstanding the fact that many eucheumatoid cultivars are presently (and consistently) recognized by the Filipino farmers, there has been no attempt to summarize the current state of the local traditional knowledge about the diversity of this seaweed group, especially with reference to the taxonomy, cultivar designation and distribution. Factors based on present day local knowledge on the eucheumatoid cultivars and what is known on genetic identification in the Philippines were also discussed. A total of 66 cultivars recognized across 58 provinces in the Philippines were documented. Most of these cultivars were morphologically identified as either *K. alvarezii* or *K. striatus*, however, the majority were yet to be genetically identified. In part, due to higher demand of kappa-carrageenan extract as compared from the iota type, *K. alvarezii* and *K. striatus* were widely cultivated in the Philippines than that of *E. denticulatum*. Only in the southern Philippines that *K. malesianus* is currently cultivated. The diverse cultivars identified in this study suggest that the Filipino farmers possess important traditional knowledge that can be useful for future crop selection and breeding.

KEYWORDS

Carrageenophytes; distribution; ethnobotany; seaweed farming; taxonomy

Introduction

The establishment of mariculture economies based upon farmed seaweeds began independently across the globe (Critchley and Ohno 1998). Seaweeds currently comprise a significant portion of the world's aquaculture production, with over 32 million tonnes of fresh weight harvested in 2018 (Chopin and Tacon 2021; FAO 2020). Evolving pressures, based on commercially driven practices, has led to the increase effects of diseases and pests and are compounded by growing environmental challenges (changing climate, pollution, coastal use conflicts, etc.). This brings into

question the present farming practices and calls forth the establishment of global surveillance systems to address tradeoffs between climate change and food security (Naylor et al. 2021). Sustainable and high yield production has, however, become a critical factor in the further successful development of this global industry.

The term 'phyconomy' was coined by Hurtado et al. (2019) to describe a unified concept of extensive and sustainable seaweed farming for livelihood purposes. Coupled with economic benefits are the legacies that phyconomy has rendered to human histories, especially on redefining demographics of coastal settle-

ments (Hussin and Khoso 2021; Nimmo 1986; Nor et al. 2017) and promoting in the industry (Larson et al. 2021; Msuya and Hurtado 2017; Periyasamy et al. 2014; Valderrama et al. 2013). Today, seaweed farming is not only seen as a food crop enterprise, but also as a multi-use system with significant potential for ecosystem services such as carbon capture to mitigate ocean acidification (Duarte et al. 2017; Froehlich et al. 2019; Xiao et al. 2021), aid in eutrophic environment restoration (Narvarte et al. 2022; Roleda and Hurd 2019) and provide an eco-engineering solution for problems on urban shorelines (Heery et al. 2020).

Species belonging to the rhodophyte genera *Kappaphycus* and *Eucheuma*, collectively known as eucheumatoids, are the major sources of carrageenans. Carrageenans are commonly used as processed food ingredients. The various types of carrageenans are composed of high molecular weight sulfated hydrocolloid molecules that are added to other foods as gelling, thickening, and stabilizing agents (Guo et al. 2022). Some of the physical properties of carrageenans have been used recently as effective encapsulating agents (Dong et al. 2021; Jana et al. 2022), and for anti-viral properties (Derby et al. 2018; Jang et al. 2021). Evidence imposing health risks of carrageenans have however rendered moot about the confusion between poligeenan (a possible human carcinogen) with native carrageenans and the modes of the administration used (Bhattacharyya et al. 2019; David et al. 2018; McKim et al. 2019). The huge database around the use and benefits of carrageenans will certainly continue to drive path to the success of providing unique solutions to various human use, particularly in health promotion (Frediansyah 2021; Jayakody et al. 2022; Liu et al. 2021).

The eucheumatoids were in part, initially cultivated in the Philippines to support a carrageenan industry suffering from decline in wild collections, and to produce more stable and uniform product (Blanchetti-Revelli 1995; Kraft 1997). Selection of fast-growing clones of eucheumatoids from wild stocks by pioneering Filipino farmers (Doty and Alvarez 1975) and the successful establishment of farms in the 1970s led to the rapid adoption and expansion of seaweed farming in the Philippines (Trono and Largo 2019, see also Figure 1). There are currently 58 coastal provinces engaged in seaweed farming in the country (Figure 1). Local and seasonal changes in environmental conditions (e.g. seasonal typhoons) and farming problems (e.g. diseases and pests) can influence crop production and as a result, a number of local farming customs have been developed including selection of cultivars (i.e. after exchange of cultivars between the Filipino farmers),

cropping calendars (i.e. selecting growing season and harvesting time to maximize production), type of planting and drying methods (Hurtado et al. 2019; Quiaoit et al. 2016).

Seaweed cultivar traits are either preexisting (from their evolutionary history) or have arisen during the domestication process through breeding and artificial selection (Valero et al. 2017). Deliberate or unintentional artificial selection may drive the ability of cultivars to improve or maintain high productivity despite varying environments (Charrier et al. 2015; Hwang et al. 2019; Kluyver et al. 2017). The selected eucheumatoid cultivars typically exhibit traits that favor high biomass production and qualities, such as carrageenan yield and gel strength (Parenrengi et al. 2020; Phang et al. 2010; Trono et al. 2000). The cultivation in eucheumatoids is done through asexual or vegetative propagation. There is no breeding (as in sexual crosses) ever done, however rare reports of sexually reproductive individuals were observed at farm sites (see Azanza-Corrales et al. 1992). Farmers may have been long selecting introgressed individuals unintentionally, allowing combinations of superior eucheumatoid cultivars.

It has been suggested that a classification system based on the information imparted by the farmers can serve as a starting point for assessing the diversity of crop cultivars, such as observed in maize (Hopkins 2006), potato (de Haan et al. 2007), rice (Loko et al. 2021; Wang et al. 2016), banana (Chabi et al. 2018; Nantale et al. 2008) and yam (Asfaw et al. 2021). For eucheumatoid cultivars, improving knowledge on genetic and phenotypic diversity could help identify suitable candidates for strain amelioration and increase resiliency to disease or pest outbreaks, and to multiple stressor effects associated to climate change (Faisan et al. 2021; Hinaloc and Roleda 2021; Largo et al. 2017; Ward et al. 2020, 2022). The innate effectiveness of seaweed cultivars in terms of production is demonstrably enhanced when combined with other means of improving pathogen control and thermal tolerance such as DNA fingerprinting, genetic assessment, hybridization and thermal priming (Hu et al. 2021; Hwang et al. 2019; Jueterbock et al. 2021). Knowledge on farming practices and the diversity of cultivars, in combination with the application of breeding programs, can be used as a valuable reference in national planning initiatives in providing effective policy frameworks to sustainably develop the industry (Brakel et al. 2021; Cottier-Cook et al. 2016).

The seaweed cultivars initially identified for commercial exploitation in the Philippines (Doty 1973; Doty and Alvarez 1973; Parker 1974) have now been distributed worldwide, due to easy vegetative

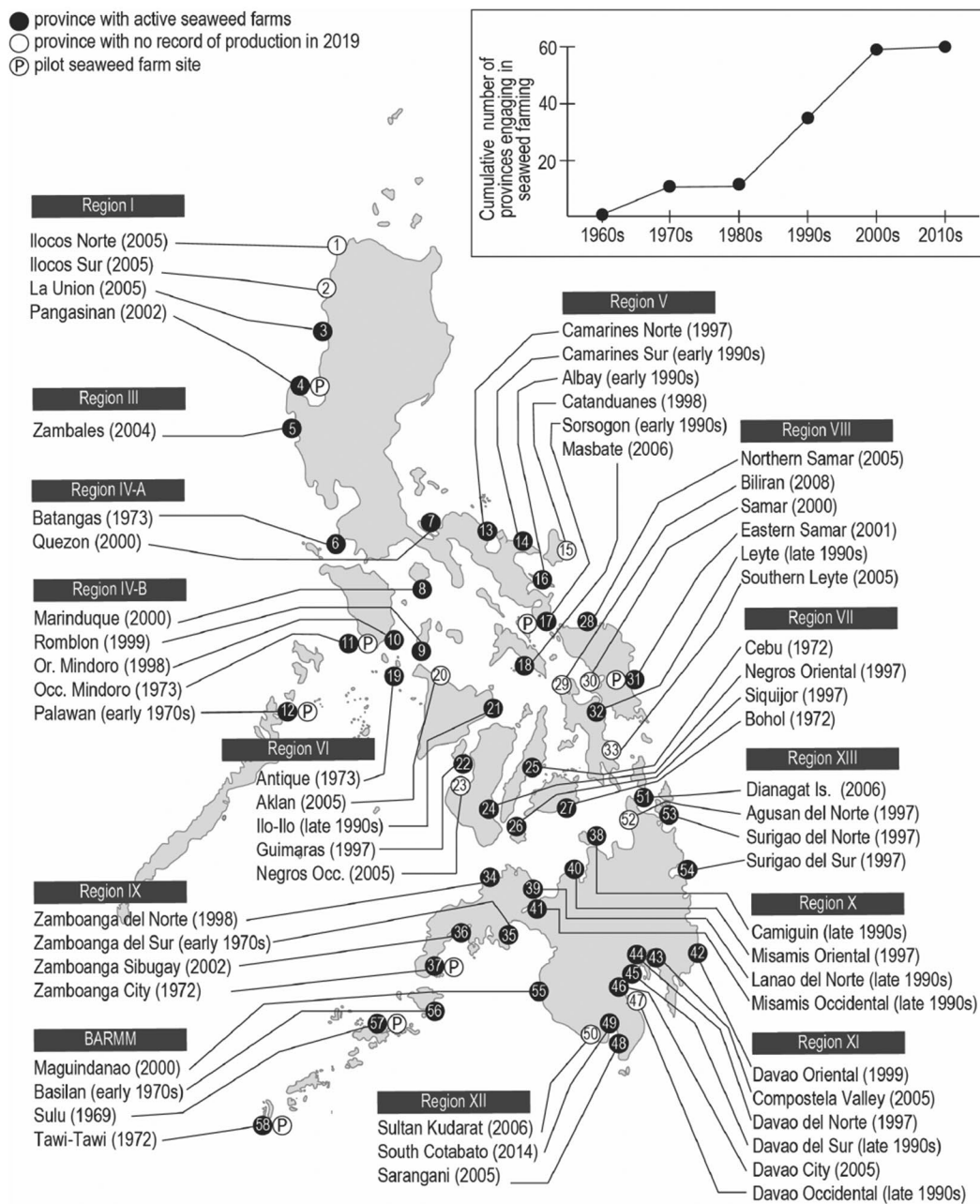


Figure 1. Distribution of seaweed eucheumatoid farms in the Philippines. The cumulative number of provinces in the Philippines engaging in seaweed farming has increased since its inception in the late 1960s (inset).

propagation (Kelly et al. 2020; Neish et al. 2017). From over the five decades of seaweed farming, Filipino farmers have accumulated extensive knowledge on farming practices and cultivar selection (Mateo et al. 2021; Suyo et al. 2021). Despite the long history of seaweed farming in the Philippines, the diversity, and distribution of seaweed cultivars as recognized locally in the country have not been thoroughly reviewed. The current contribution aims to review the taxonomy, diversity, and distribution of eucheumatoid cultivars, as well as their genetic differentiation and conservation strategies in the Philippines.

Literature review

A systematic review was conducted of peer-reviewed journal articles, local books, and unpublished lists that mention local names of eucheumatoid cultivars identified by the Filipino farmers. Species identification of these cultivars were determined by either consulting the farmers directly or, if previously reported, by assessing the original reporting sources. The cultivars were identified based on the species recognized by each of the sourced authors, local names that were used by other authors to refer to a

similar cultivar name, cultivar name etymologies, and their distribution in the Philippines. Translation and interpretation of the meanings of the local names were provided by the farmers or expert native speakers. The reported *cox2-3* spacer barcodes of eucheumatoids from the Philippines were also gathered from existing literature.

Nomenclatural note

The terms *cultivar*, *strain*, and *variety* are commonly used interchangeably in differentiating morphological diversities among algae, particularly in seaweed crops. The term *strain* may either refer to a wild or cultivated eucheumatoid. The name of a strain can be derived from a name used by the farmers, or a name assigned by the investigator (e.g. on the basis of a replicate) generally used for experimental studies (see Ali et al. 2018; Hayashi et al. 2007; Mendoza et al. 2002). In this review, only the term *cultivar* will be used to the seaweed crops grown and named by the farmers in accord with the definition of the International Code of Nomenclature for Cultivated Plants (Brickell et al. 2016). Likewise, as specified in the International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al. 2018), the use of the term *variety* in this study will pertain to a variation below species level effected by a valid taxonomic description.

Taxonomy of eucheumatoid seaweed cultivars in the Philippines

Eucheumatoid seaweeds (tribe Eucheumatoideae, family Solieriaceae, order Gigartinales, phylum Rhodophyta) represent the majority of farmed species in the Philippines (Doty 1988). The tribe Eucheumatoideae originally contained three genera: *Eucheuma*, *Kappaphycus*, and *Betaphycus* (Doty 1988, 1995). Recent phylogenomic reconstruction based on 21 mitochondrial genomes suggests that the three genera form a clade (Li et al. 2018). Current molecular phylogenetic analyses inferred within the Eucheumatoideae has now led to the addition of three more genera, *Tacanoosca* (Norris 2014), *Eucheumatopsis* (Núñez-Resendiz et al. 2019), and *Mimica* (Santiañez and Wynne 2020), each segregated from *Eucheuma sensu lato*.

Although phylogenetic radiation within the tribe has been hypothesized to have occurred in the ancient Tethys Ocean prior to continental shifts some 100 MYA (Fredericq et al. 1999), the highest

eucheumatoid diversity is currently reported in the Indo-Pacific (Doty 1988; Hurtado et al. 2016). Members of the eucheumatoids are found growing in a variety of habitats from shallow reefs to depths of over 45 m (Doty 1973). As a consequence of intentional transplantations that have taken place for farming uses, eucheumatoids are also now established in many non-indigenous regions characterized by warm waters of Atlantic (Brakel et al. 2021; Kelly et al. 2020).

The farmed eucheumatoids in the Philippines include *Eucheuma denticulatum*, *Kappaphycus alvarezii*, *Kappaphycus malesianus*, and *Kappaphycus striatus* (Figures 2 and 3). Morphologically, these taxa are characterized by a set of several overlapping characters (Doty 1988; Hurtado et al. 2016; Tan et al. 2014) that make definitive identification difficult at times. Progress on the phylogeny and taxonomy in this group has been enhanced by the use of molecular data (Dumilag et al. 2016a; Lim et al. 2017; Tan et al. 2012; Zuccarello et al. 2006). Despite the considerable morphological diversity that domesticated eucheumatoids display, there are only four taxonomic varieties recognized. These include *Eucheuma denticulatum* var. *endong* (Ganzon-Fortes et al. 2012), *Kappaphycus alvarezii* var. *alvarezii*, *Kappaphycus alvarezii* var. *tambalangii* and *Kappaphycus alvarezii* var. *ajakii-assii* (Liao 1996). Except for *K. alvarezii* var. *alvarezii* (type locality is in Malaysia), the Philippines is the type locality of all these varieties (Doty 1985).

Commercial nomenclature in eucheumatoids

Far predating the advent of their domestication, the use of seaweeds as food in the Philippines has a history dating back to pre-colonial occupation of the islands (Velasquez 1977). The earliest Philippine record of seaweed as a trade commodity began in the seventeenth century when *Agal-agal*, a local name for eucheumatoids, was recorded as a major food product (dried and fresh seaweeds) in the early Sulu enterprises and as an exchange commodity for imports from China (Fry 1970; Saleeby 1908). In 1704, Georg Joseph Kamel, S.J., the Jesuit missionary and apothecary based in Manila, mentioned an abundant marine commodity locally called *goso* which undoubtedly referred to various eucheumatoids back then as well as now (Liao 2013). Eucheumatoids have since remained a highly sought after seaweed products, with deep cultural value among communities in the Philippines (Dumilag 2019).

Stable nomenclature for products is necessary for communication and record keeping regarding

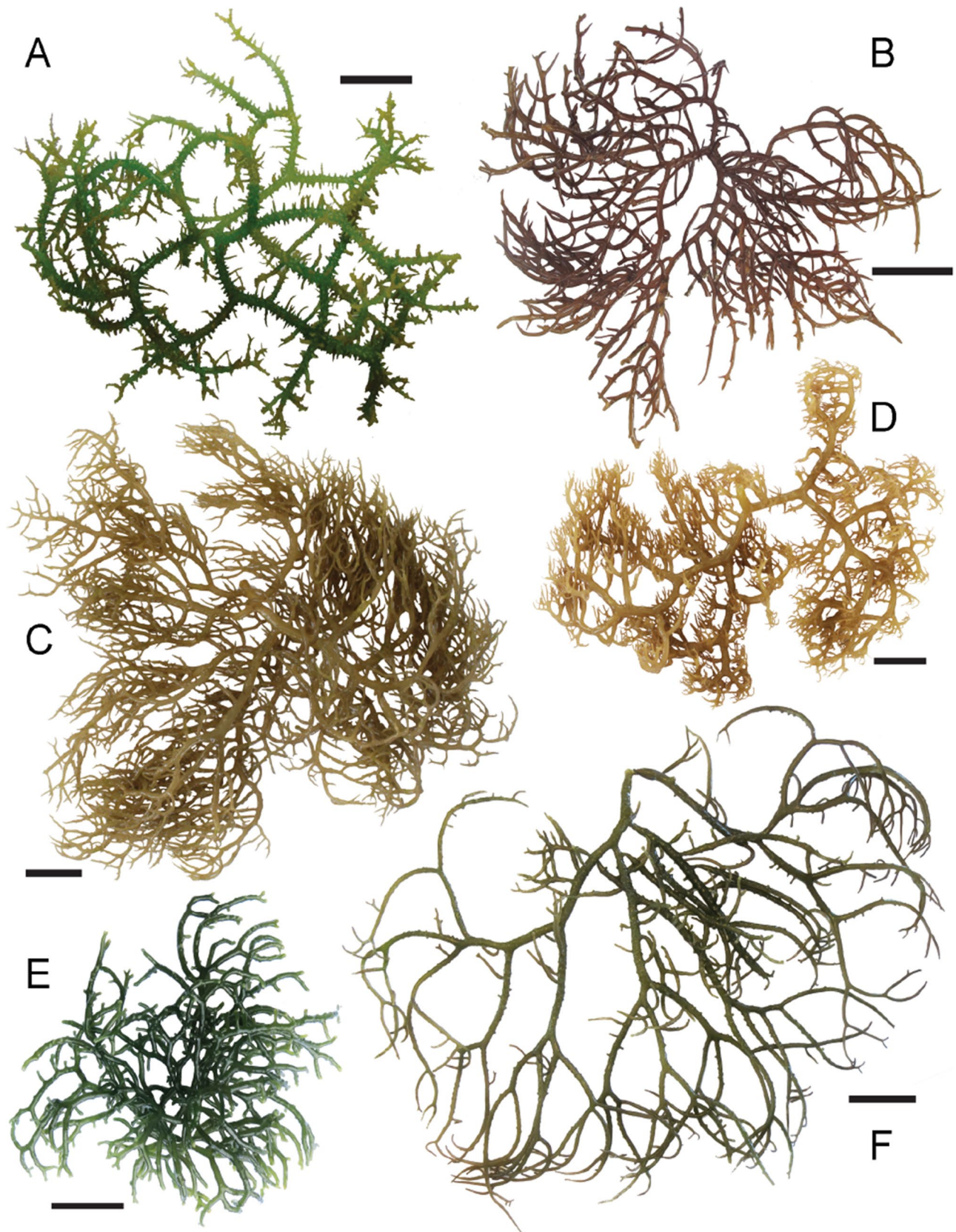


Figure 2. Philippine *E. denticulatum* and *K. alvarezii* cultivars. *E. denticulatum* cultivars *Spinosum* (A) from Cebu and *Milyon-Milyon* (B) from Batangas. *K. alvarezii* cultivars *Tambalang* (C) and *Marimar* (D) from Tawi-Tawi, *Digos* (E) and *Giant* (F) from Surigao del Sur. Scale bars: A: 5 cm, B: 3 cm, C: 5 cm, D: 3 cm, E: 3 cm, F: 12 cm.

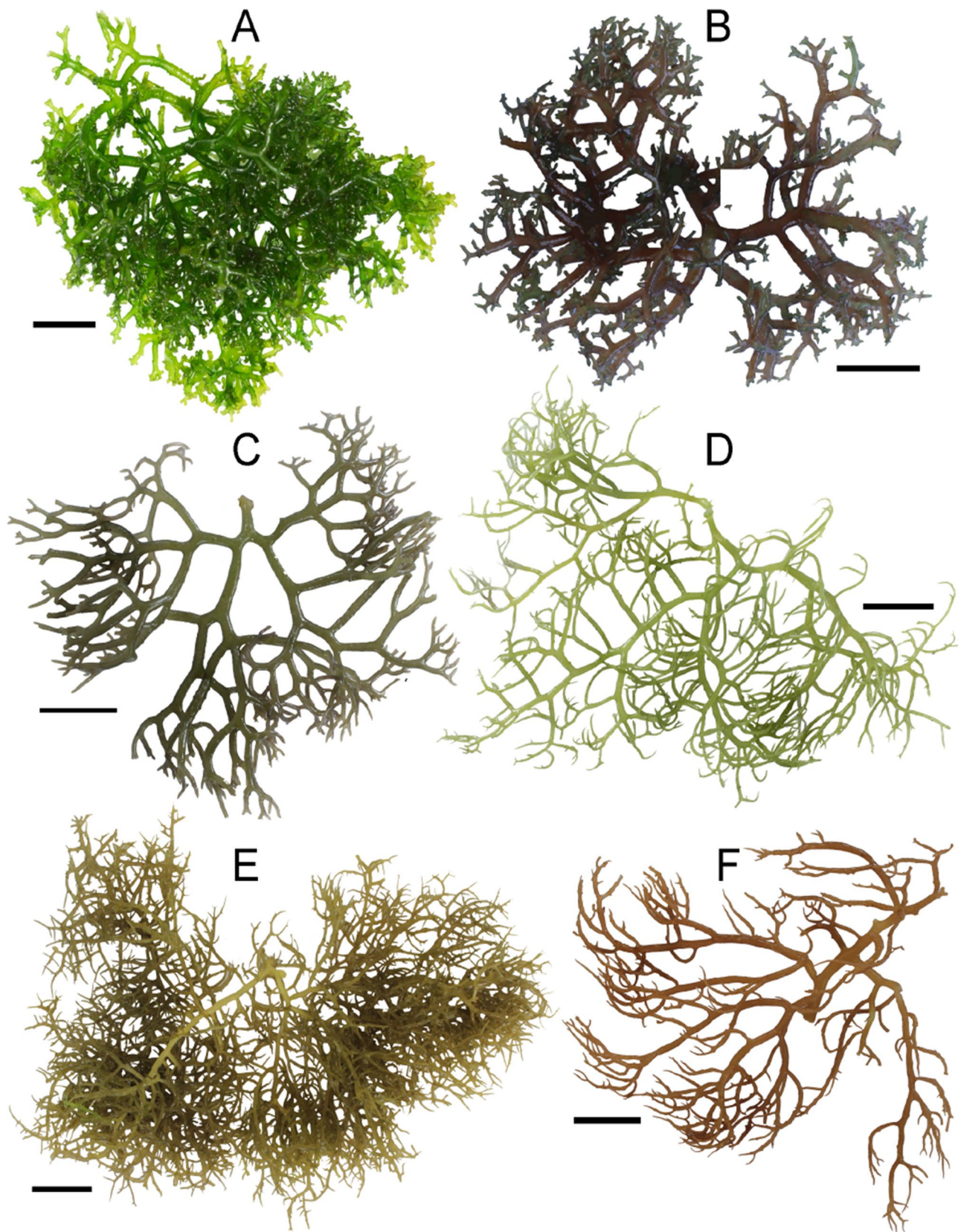


Figure 3. Philippine *K. striatus* and *K. malesianus* cultivars. *K. striatus* cultivars Sacol (A) from Batangas, *Seven Colors* (B) from Tawi-Tawi, *Kab-Kab* (C) from Zamboanga City. *K. malesianus* cultivars *Aring-Aring* (D), *Halaw* (E) and *Kuku Belleh'* (F) from Tawi-Tawi. Scale bars: A: 3 cm, B: 3 cm, C: 5 cm, D: 3 cm, E: 3 cm, F: 6 cm.

biological resources and their acceptance for trading purposes. The standard use of names is also essential to various scientific applications as there can be mixing of euclidean species belonging to different genera. This leads to mixed carrageenan extracts, lowering the quality of the final product (see Ganzon-Fortes et al. 2012). Since the 1980s, taxonomists have been aware of the significant confusion that exists in relation to the correct scientific epithets for commercially important seaweeds (Bolton 2020), including of euclidean (Dumilag et al. 2020, Table 1). The situation is compounded in euclidean, as some investigators continue to publish their work using outdated nomenclature, e.g. the use of “*Euclidean cottonii*” (see Mansa et al. 2013; Matanjun et al. 2009; Purbosari et al. 2021 Surya et al. 2021; Teo et al. 2021), “*Euclidean spinosum*” (see Bouanati et al. 2020, Gurav et al. 2021) and even a non-existent taxonomic combination, “*Kappaphycus spinosum*” (see Adharini et al. 2019). This highlights the importance of proactive assessment and intervention by journal editors and expert reviewers, particularly in applied sciences where reports of invalid species names are prevalent (c.f. Roleda et al. 2021b; Roleda and Heesch 2021) and are most often left uncorrected, except on rare occasions (e.g. Roleda et al. 2021c).

Diversity of Philippine euclidean cultivars based on local knowledge

Sixty-six euclidean cultivars were identified and named in the Philippines, largely based on morphology recognized by Filipino farmers (Table 2). Twenty-seven cultivars were identified as *K. alvarezii*, 15 as *K. striatus*, six as *E. denticulatum* and three as *K. malesianus*. Fifteen cultivar names required further investigation to determine what species they belong to. The majority (83%) of cultivar names were identified as a single species while others were attributed to more than one taxa. For example, the cultivar *Aring-Aring* was represented by all three farmed *Kappaphycus* species while the cultivars

Cottonii (or *Katunay*) and *Sacol* may be attributed to either *K. alvarezii* or *K. striatus*. Even the *Spinosum*, the most common cultivar name for *E. denticulatum*, can be referred to as a cultivar of *K. alvarezii* (Table 2).

Local cultivars were structurally named, using either a unitary (single word) or a binary (two words) format. Unitary names predominated, constituting 62 of the 66 cultivars identified by farmers. Of these, 83% were derived from local dialects, while the others were adapted from English. Some unitary names were formed through full lexical reduplication (i.e. repeating names such as *Milyon-Milyon*, *Kab-Kab*, *Butay-Butay*), a familiar word formation process among Philippine language (Blake 1917; Mattes 2014; Rubino 2005). With the exception of the cultivars *Ara Mina* and *Kuku Belleh*, the others had binary names adapted from English (e.g. *Nile Green*, *Sweet Loving* and *Seven Colors*).

The translation of the names used revealed that most cultivar names matched certain aspects of the seaweed. The name derivations were based on several attributes, or objects, such as the description of the general branching pattern (e.g. *Endong* is a worm-like, *Kab-Kab* is a fan-like, and *Repolyo* is a cauliflower-like), color (e.g. *Nile Green*, *Pula-Pula* [red], and *Seven Colors*), source locality (e.g. *Digos*, *Sacol*, and *Zamboanga*) and the person who discovered them (e.g. *Aring-Aring* and *Tambalang*). Only a few names had no clear reference as to the characteristics or history of the origin, e.g. some cultivars were named from popular personalities (e.g. *Ara Mina* and *Marimar*, popular actresses), or random brand names (e.g. *Duralex*, *Bitsi-Bitsi* from Mitsubishi, and *Vanguard*, brand names relating to boats). Two cultivars have unknown etymologies (i.e. *Sweet Loving* and *Way-Way*).

Eighteen cultivars had variant names (Table 2). The cultivar *Tambalang* (Figure 3C) had the greatest number of variants with 14 name combinations. Color was the most common trait attributed to a variant name (see also Hurtado 2013). Brown, green, and red were found to be the dominant colors of seaweed cultivars in the Philippines (Figure 4). The species

Table 1. Commercial names of farmed euclidean species in the Philippines.

Extracted carrageenan	Commercial name	Taxonomic name		Commonly confused species name
		Currently accepted species	Common Synonym	
beta-carrageenan	serra	<i>Betaphycus gelatinus</i>	<i>Euclidean gelatinae</i> <i>Betaphycus gelatinum</i> <i>Betaphycus philippinensis</i>	<i>Euclidean serra</i> ¹ <i>Euclidean perplexum</i> ¹
iota-carrageenan kappa-carrageenan	spinosum cottonii	<i>Euclidean denticulatum</i> <i>Kappaphycus alvarezii</i> <i>Kappaphycus malesianus</i> <i>Kappaphycus striatus</i>	<i>Euclidean spinosum</i> <i>Euclidean alvarezii</i> <i>Euclidean striatum</i>	<i>Euclidean serra</i> <i>Kappaphycus cottonii</i> ² (as <i>Euclidean cottonii</i>)

Non-domesticated euclidean species producing ¹iota- or ²kappa-carrageenan. See details on Dumilag et al. (2020).

Table 2. A list of euclidean cultivars identified and named by Filipino farmers, including their etymology, *cox* 2-3 spacer haplotype assignment and distribution.

Local Name (variant)	Etymology (dialect)	<i>cox</i> 2-3 spacer haplotype	Philippine distribution
<i>E. denticulatum</i>			
Endong, Spaghetti (br, gr)	worm-like (Sama)		17 ^a , 27 ^b , 58 ^b
Korea	as the country		37 ^c
Spinusum (br, gr)	spinous morphology	13 ^d	5 ^b , 6 ^b , 10 ^b , 12 ^b , 17 ^b , 18 ^b , 19 ^b , 21 ^b , 22 ^b , 24 ^b , 25 ^b , 27 ^d , 28 ^b , 32 ^b , 33 ^b , 36 ^b , 37 ^b , 42 ^b , 45 ^b , 46 ^b , 51 ^b , 54 ^b , 57 ^b , 58 ^b
Milyon-Milyon	presence of numerous branches (Tagalog, derived from the English word million)		6 ^b , 11 ^b , 12 ^b , 19 ^b , 22 ^b , 27 ^b , 37 ^b
Nile green	refers to its color		45 ^b , 48 ^b , 47 ^b
Zamboanga	the province of its origin, Zamboanga		54 ^b
<i>K. alvarezii</i>			
Adik-Adik /Adis-Adis (br, gr, rd)	refers to a junkie, a drug addict (Bisayan pop culture)		35 ^b , 37 ^{b,ef} , 45 ^b , 46 ^b
Aring-Aring (br, gr)	after Mr. Joe Aring, the owner of large seaweed farms in Umapoy Is., Sibutu, Tawi-Tawi	3 ^g	17 ^g , 58 ^c
Barako	boar, related to a local coffee from Batangas, origin may be from this area (Tagalog)	3 ^h	22 ^{b,h}
Bermuda	refers to its color, Bermuda green	3 ^h	42 ^b , 53 ^b , 54 ^{b,h}
Burikat (br, gr)	to open one's legs wide (Bisaya)	KALV-1 (br) ^h KALV-2 (gr) ^h	35 ^b , 54 ^h
Cottonii, Katunay (br, gr)	named after Arthur Disbrowe Cotton, an English botanist who supplied Anna Antoinette Weber van Bosse the specimens used to describe <i>Kappaphycus cottonii</i> – katunay is an onomatopoeic form of 'cottonii'	3 ^d	4 ^b , 5 ^b , 7 ^b , 13 ^b , 18 ^b , 17 ^b , 19 ^b , 22 ^b , 25 ^b , 27 ^{b,d} , 28 ^b , 31 ^b , 34 ^b , 35 ^b , 36 ^b , 37 ^b , 42 ^b , 44 ^b , 45 ^b , 53 ^b , 54 ^b , 57 ^b , 58 ^c
Digos (br, gr)	its area of origin, Digos City, Davao del Sur	3 ^h	54 ^h
Giant (kapilaran, original)	pertains to its large size	3 ^h KALV-1 ^h	12 ^b , 25 ^f , 28 ^b , 31 ^b , 32 ^b , 33 ^b , 34 ^b , 35 ^b , 36 ^b , 37 ^{b,f} , 53 ^b , 54 ^{b,h} , 58 ^{b,h}
Gulaman	anything jelly (Tagalog)		18 ^b , 30 ^b , 31 ^b
Jackpot, Swerte	lucky (English, Spanish)		58 ^b
Kab-Kab, Pay-Pay	fan-like (Tausug)	3 ^d	35 ^b , 37 ^d , 58 ^b
Kinangkong, Natural, Plastic	water spinach-like, vegetable-like (Tagalog)		13 ^b , 14 ^b
Kinse-Kinse	refers to fifteen days before harvest (Spanish 'quince')		11 ^b , 12 ^b , 58 ^c
Kulot	curly (Tagalog)		37 ^b , 58 ^c
Lakway	from 'lakaw' means to walk (Bisaya)		43 ^b , 44 ^b , 54 ^b
Marimar	a famous 1990s Mexican soap opera released in the Philippines under the same title	3 ^h	58 ^h
Milo-Milo, Milo	a popular brand of cocoa drink, referring to its branch color	3 ⁱ	35 ^b , 37 ⁱ , 58 ^b
Patig	from 'fatigue', a khaki-olive green military suit		58 ^c
Pula-Pula	red (Tagalog, Bisaya)		58 ^c
Putan	from the same name of a Sama local sticky rice cake. Its brown color matches that of the cultivar's branches (Tausug)		58 ^c
Tambalang (abu [gy], adik, batu [rock], br, diki [small], giant, heya [big], milo, monten [mountain], pu, lapsi, rd, sacol, tunay [shortened from Katunay])	derived from the owner of the farm, Mr. Tambalang Bin Panggian from Sitangkai	3 ^d	6 ^b , 7 ^b , 12 ^b , 14 ^b , 16 ^b , 18 ^b , 22 ^b , 25 ^h , 35 ^b , 37 ^h , 40 ^b , 42 ^b , 43 ^b , 44 ^b , 45 ^b , 46 ^b , 47 ^b , 48 ^b , 57 ^b , 58 ^{b,c,d}
Tungawan	a municipality in Zamboanga Sibugay		22 ^j
Spinusum (br, gr)	spinous morphology	3 ^h	54 ^h
Sweet Loving	unknown etymology		58 ^b
Sacol (rd, vanguard)	an island in Zamboanga City	3 ^d	12 ^c , 37 ^{d,k}
Vanguard	from the brand name of the machine, Vanguard, bought by a seaweed farmer after his good harvest	3 ^d	37 ^d
Way-Way	unknown entity		39 ^b , 41 ^b , 36 ^b ,
<i>K. malesianus</i>			
Aring-Aring	from Mr. Joe Aring, the owner of large seaweed farms in Umapoy Is., Sibutu, Tawi-Tawi		58 ^b
Halaw	illegal Filipino deportees to borders of Malaysia (Tausug/Sama)	MY216 ^h	58 ^h
Kuku Belleh'	talon of an eagle (Sama)	MY216 ^h	58 ^h

(Continued)

Table 2. (Continued)

Local Name (variant)	Etymology (dialect)	cox2-3 spacer haplotype	Philippine distribution
<i>K. striatus</i>			
Aring-Aring (br, gr)	from Mr. Joe Aring, the owner of large seaweed farms in Umapoy Is., Sibutu, Tawi-Tawi	89 ^g	17^g
Bitsi-Bitsi, Bitsi (gr)	from the corrupted name of a boat engine brand, Mitsubishi	89 ^h	58^h
Bola-Bola	ball-like (Tagalog)		25 ^b , 28 ^b
Bukoy-Bukoy	a name of a child, presumably from Palawan		12 ^{b,c}
Cottonii, Katunay (bl, br, gr, rd, sacol)	named after Arthur Disbrowe Cotton, an English botanist who supplied Anna Antoinette Weber van Bosse the specimens used to describe <i>Kappaphycus cottonii</i>	89 ^d	17 ^b , 22 ^b , 27^{b,d} , 57 ^b , 58^{b,d}
Duyan-Duyan (br, gr, rd)	hammock-like (Tagalog)		48 ^b , 57 ^b , 58 ^b
Emo (br, gr)	presumably a name of a farmer who first used it from Zamboanga, Mr. Emo	89 ^h	37^h
Jackpot, Swerte	lucky (English, Spanish)	89 ^h	58^h
Jayan-Jayan	giant-like, an onomatopoeic form of 'giant' from English		58 ^c
Kab-Kab, Paypay (br, gr)	fan-like (Tausug/Sama, Tagalog, Bisaya)	89 (gr) ^h , 117 (br) ^h	35 ^b , 58^{b,d,h}
Payaka, Yaka	squatting posture or form (Bisaya)		25 ^b , 32 ^b , 53 ^b
Sacol, Cauliflower, Flower, Repolyo (br, gr, or)	the area of its origin, Sacol Is., Zamboanga, cabbage-like (Tagalog)	89 ^{d,h}	6^{b,h} , 12 ^b , 17 ^b , 19 ^b , 21 ^b , 22^{b,h} , 25 ^b , 28 ^b , 35 ^b , 37^{b,d,h,f} , 53 ^b , 57 ^b
Seven Colors	pertains to the seven colors of its branches		58 ^{b,c}
Subul/Subol-Subol (br, gr, rd)	a young male (Tausug)		58 ^c
Vanguard, Banggard	derived from the name of a boat engine brand; Banggard is a spelling variant of Vanguard	89 ^h	5 ^b , 11 ^b , 12 ^b , 18 ^b , 25 ^b , 27 ^b , 28 ^b , 34 ^b , 35 ^b , 39 ^b , 41 ^b , 53 ^b , 58^{b,h}
Unknown species			
Ara Mina	screen name of Hazel Pascual Reyes, a popular Philippine actress		36 ^b , 37 ^b
Bisaya	the local people from Visayas region		27 ^k
Bulawan	golden (Tausug, Bisaya)		12 ^b
Butay-Butay	like a coconut leaf midrib (Cebuano)		27 ^b
Dayang-Dayang	a princess (Tausug/Sama)		25 ^b
Dugong	<i>Dugong dugon</i> , the sirenian		43 ^b , 44 ^b
Duralux	from the corrupted name of a marine paint brand, Duralux		35 ^b
Durian	from <i>Durio zibethinus</i> , the strongly aromatic fruit in SE Asia		58 ^{b,c}
Marlin	a fish belonging to family Istiophoridae		37 ^l
Original	originally sourced from Antique province only		19 ^b
Polotan	any food eaten without rice (Tagalog)		35 ^b
Sakot	ingredient (Bisaya)		19 ^b
Sparkle	pertaining to its green color		58 ^c
Sprite	a popular soft drink brand, inspired by the similar green color of its bottle		12 ^b
Tangtang-utang	literally dropping of debt (Bisaya)		37 ^c

bold numbers indicate site of collection of DNA barcoded specimen/s.

bl: black, br: brown, gr: green, gy: gray, or: orange, pu: purple, rd: red.

^aGanzon-Fortes et al. 2012.

^bQuiaoit et al. 2016.

^cThis study.

^dLim et al. 2014.

^eHurtado and Biter 2007.

^fHurtado et al. 2009.

^gDumilag and Lluisma 2014.

^hDumilag et al. 2016a.

ⁱTan et al. 2012.

^jBorlongan et al. 2011.

^kHurtado 2013.

^lSuyo et al. 2020.

with most color variability was *K. striatus*. Several individuals of the *E. denticulatum* cultivar *Spinusum* (Figure 2A) exhibited bi-colored (brown and red) thalli. This similar color pattern was observed in specimens (referred to as ecotypes) sampled from varying environments suggest that it may have a genetic basis, as previously shown in gracilarioids (e.g. Marchi and

Plastino 2020; Plastino et al. 1999; van der Meer 1979). Accordingly, the green and brown color variants of *K. alvarezii* cultivar *Burikat* and *K. striatus* cultivar *Kab-Kab* (Figure 3C) each had differing *cox2-3* spacer haplotypes (Dumilag et al. 2016a, see Table 2). Mention of variation in pigmentation was rare in eucheumatoid cultivars while this type of trait

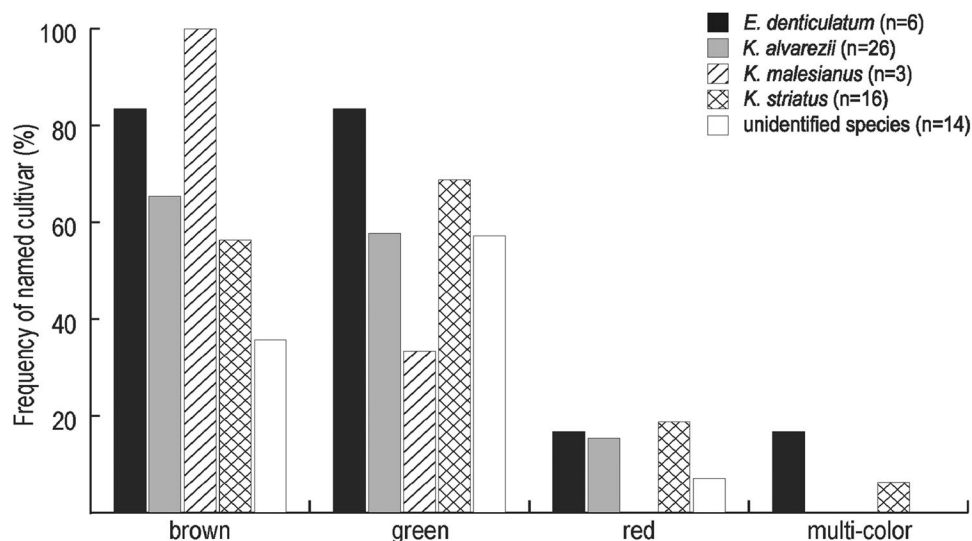


Figure 4. Percentage frequency of seaweed cultivars corresponding to their thallus color. The number of identified cultivars (n) is denoted per species.

was important in the description for some cultivars. Accordingly, the *K. striatus* cultivar *Seven Colors* (only recorded in Tawi-Tawi, southern Philippines to date, see Figure 3B) cannot be categorized as one discrete color, since the thallus was multi-colored ranging from yellow, to green to brown. If other cultivars had exhibited pigment variation comparable to *Seven Colors*, seaweed farmers would probably have used it as a distinguishing character. Other variant identification features were based on a combination of other cultivar names, e.g. *Tambalang Giant*, *Tambalang Sacol*, *Sacol Vanguard* or size differences, e.g. *Tambalang diki* (small) and *Tambalang heya* (big).

The basis behind the pigment expression in eucaeumatoids is not well understood. Recently, wild reproductive *K. alvarezii* (cystocarpic and tetrasporic) were observed to exhibit mosaic pigmentation on the same branch. The resulting tetrasporophyte progeny expressed the same mosaic pigmentation as their parent, while the gametophyte progeny expressed different colors (Hinaloc and Roleda 2021). Expression of mosaic pattern of pigmentation in eucaeumatoids may have resulted from the coalescence of “genetically-distinct” spores (chimeric plants) as reported in *Gracilaria chilensis* (Santelices et al. 2017) and *Neopyropia yezoensis* (Niwa and Abe 2012).

Distribution of eucaeumatoid cultivars in the Philippines

The eucaeumatoid species and the corresponding distribution of cultivars in the Philippines appeared to be random (Figure 5, Table 2). Twenty-six of the

named cultivars were recorded in multiple areas throughout the country. Forty cultivars were exclusive to a single area, particularly in Regions IX and XIII, and BARMM. The highest number of cultivars were found within the larger farming areas, including Tawi-Tawi (BARMM, n = 30), Zamboanga City and Zamboanga del Sur (Region IX, n = 17 and n = 12 respectively), and Palawan (Region IV-B, n = 11). The cultivar named *Spinosum* (Figure 2A) was found to be the most widely distributed of the *E. denticulatum*. The *Cottonii*, *Tambalang* (Figure 2C) and *Giant* (Figure 2F) accounted for the three most common *K. alvarezii* cultivars. *Sacol* (Figure 3A) and *Vanguard* were the most common for *K. striatus*. Only being reported in Tawi-Tawi, *K. malesianus* had the most restricted distribution. It had three locally recognized cultivars namely *Aring-Aring* (Figure 3D), *Halaw* (Figure 3E), *Kuku Belleh'* (Figure 3F). Nearly all of those cultivars that have yet to be identified by scientific names are only known from their respective areas, mostly from southern Mindanao.

Selection of eucaeumatoid cultivars in the Philippines is most often related to the type of carrageenan, robustness (against environmental stressors, pest, and disease) and high productivity or growth rate, while other specific cultivar properties (e.g. color or branching pattern), may be nugatory to the farmers. The wide distribution of farmed *K. alvarezii* and *K. striatus* in the Philippines is due to the higher demand kappa-carrageenan extracts (i.e. as opposed to iota type carrageenan) and their reputations for greater environmental tolerance (Bindu and Levine 2011; Glenn and Doty 1992). The widespread use of cultivar names, e.g.

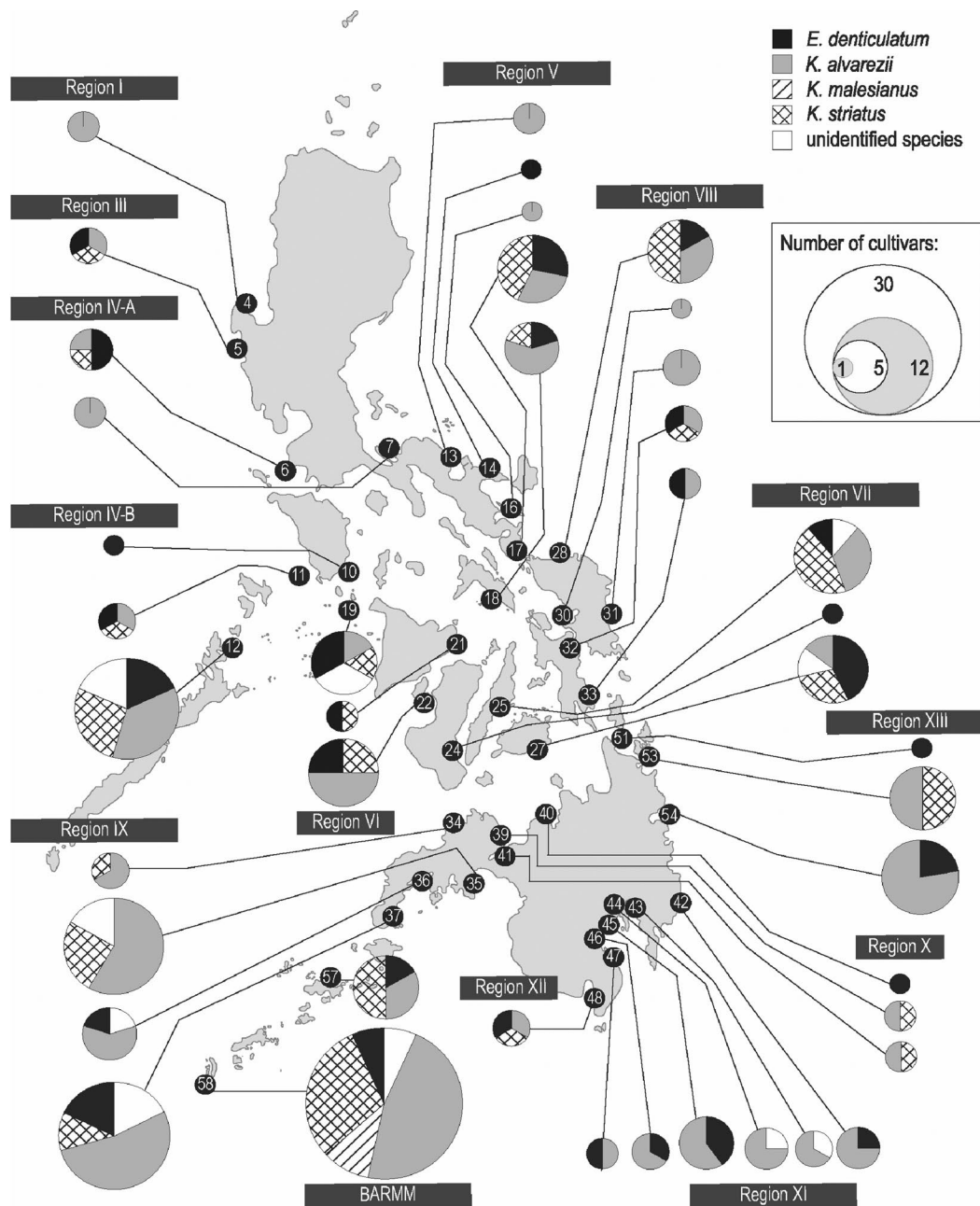


Figure 5. Distribution of seaweed cultivars in the Philippines. Pie chart represents euclidean species grown by farmers per province grouped by political region in the Philippines. Numbers indicate provinces shown in Figure 1.

Spinosum, *Tambalang*, and *Cottonii*, was most likely related to the free exchange of seedstocks across the country (see Quiaoit et al. 2016). Reciprocal transfers of cultivars was found to follow traditional community practice, as exchange occurred primarily between relatives, friends, or neighbors usually within similar ethnic groups (R. Dumilag, personal observation). Seedstocks were also exchanged after loss of crops (e.g. by typhoons or diseases and pests), during farm expansion, or when testing other cultivars for greater yields. It is therefore possible that the same cultivar names have been given to distinct farmed genotypes in

different areas. Genetic diversity is not seen by the farmers while morphological diversity may not represent genetic diversity. The information based on local knowledge may also underestimate the morphological and genetic diversity at the national, or regional level (as in case study in yam by Asfaw et al. 2021).

Typhoons are among the most severe natural disturbances seaweed farms in the Philippines ever face, i.e., rendering greatest production penalties and upsetting the dynamics of local livelihoods (Andriess and Lee 2017). The government interventions play an important role in the supply of seedstocks among

farmers, particularly after the typhoons (Cuaton 2019; Suyo et al. 2021). Farmers receive seaweed cultivars for free from the government agencies such the Department of Science and Technology (DOST), Bureau of Fisheries and Aquatic Resources (BFAR), Department of Trade and Industry (DTI) and the respective local government units (Quiaoit et al. 2016). Indonesia has overtaken the Philippines in euclidean production since 2008 (Bixler and Porse 2011). In part, this is due to the frequent exposure of the Philippines to typhoons.

Genetic diversity of Philippine euclidean cultivars

Information on genetic diversity among Philippine seaweed cultivars is still incomplete, with only 25 cultivars sequenced for mitochondrial markers. The most recent analysis based on the *cox2-3* spacer revealed that Philippine cultivars include seven haplotypes (Roleda et al. 2021a). A survey of mitochondrial *cox2-3* spacer sequences revealed between one to three farmed haplotypes per species: *E. denticulatum* (haplotype 13), *K. alvarezii* (haplotypes 3, KALV-1 and KALV-2), *K. malesianus* (haplotype MY216), and *K. striatus* (haplotypes 89 and 117). There were no clear correspondences between mitochondrial haplotypes, morphology, and cultivar names. Notwithstanding, this apparently high genetic similarity and lack of concordance between haplotypes and phenotypes, the morphological features of the different cultivars still allowed differentiation. The morphological differences also appeared to be fairly stable or were conserved between different environmental conditions, which explained how farmers were able to visually recognize each type of cultivar in the field. This observable phenotypic diversity raises the possibility that more informative genetic markers might be able to genetically differentiate between cultivars (see Risjani and Abidin 2020; Thien et al. 2020). High throughput sequencing and single nucleotide polymorphisms (SNPs) have been helpful in exploring the neutral and functional genetic diversity between terrestrial crops thereby allowing detection of misclassified cultivars, examining reduction of genetic diversity and accumulation of deleterious alleles during selection steps (Diaz-Garcia et al. 2020; O'Connor et al. 2019). These techniques might be usefully applied for euclidean cultivars in future researches.

Vegetative propagation and transfer of clones (ramets) between farms and areas impact genetic diversity in crops due to recurrent bottlenecks. The narrowing of the genetic basis begins with selection

of a few strains of interest from wild environments and is intensified during the development of elite cultivars through ongoing artificial selection. This mode of propagation dramatically affects crop genetic diversity (McKey et al. 2010; Meyer et al. 2012; Smýkal et al. 2018). In potatoes and yam for example, farming based on asexual reproduction has led to a severe reduction of genetic diversity and an accumulation of deleterious alleles (Pandey et al. 2021; Ramu et al. 2017). Although the history of domestication is more recent in seaweeds, typical impacts of extensive use of vegetative propagation in farms, include the very low levels of clonal variation, life cycle disruption, and reduction in reproductive effort as has been detected in the red alga *G. chilensis* (Guillemin et al. 2008; Usandizaga et al. 2021). The problem could be especially acute in euclidean farms where cultivation from vegetative thalli has led to the wide use of mitochondrially similar haplotypes around the world (Zuccarello et al. 2006). These farmed haplotypes have spread to adjacent areas both in the Philippines and in regions where these cultivars have been introduced (Dumilag et al. 2016b; Halling et al. 2013; Tano et al. 2015).

High genetic and phenotypic diversity is expected in naïve areas of crop origin (e.g. Hardigan et al. 2017). In the Philippines, a number of natural populations of euclidean are located near the farms and dispersal probably occurs between farmed plants and wild populations of both sporophytes and gametophytes (R. V. Dumilag, personal observation). Such conditions could help to delay the genetic diversity loss during domestication allowing introduction of new alleles at each generation even in highly asexually cultivated crops (Elias et al. 2001). Exchange of cultivars among Filipino farmers could also help to maintain large population sizes, increase genetic variation in multiple populations, but only through somatic mutations. Introgression of new alleles in crops due to natural crosses with individuals from nearby natural populations or distinct cultivars introduced from other regions could generate new genotypic combinations and potentially superior cultivars without the burden of performing costly breeding effort (Labeyrie et al. 2016; Pautasso et al. 2013). Unfortunately sexual reproduction and selection of new sporelings are uncommon practice among seaweed farmers. The continuous discovery of new euclidean haplotypes demonstrates that high genetic diversity is available in both farms and natural populations and also remain to be uncovered in the Philippines (Dumilag et al. 2016a, 2018; Roleda et al. 2021a). It is therefore

imperative to further explore this untapped diversity and to create seedbanks from sites without cultivation activity. These strategies could mitigate the decline of genetic diversity and can provide access to genetic variants better adapted to unprecedented challenges of the current seaweed farming systems. Other conservation strategies that can be applied for eucheumatoids include *ex situ* conservation such as germplasm banking through culture (De La Fuente et al. 2019; Wade et al. 2020; Watanabe 2005) and cryopreservation (Yang et al. 2021), as well as *in situ* conservation (Wambugu and Henry 2022). The high number of cultivars in the Philippines makes the region an excellent area for the discovery of new cultivars that can be preserved and their economic potential explored in future crop selection and breeding programs.

Conclusion and future directions

The extent to which the role of cultivar diversity can potentially contribute to advancing phyconomy is still largely under researched. Given the need to maintain cultivar diversity, as a means of promoting resilience of seaweed crops to disease and pests, and the increasing potential use of carrageenan and other key biomolecules in medical (Morokutti-Kurz et al. 2021; Pereira and Critchley 2020) and in some extent, to bioplastics industry (Schmidtchen et al. 2022), selection for appropriate cultivars needs to be investigated. Future studies on cultivar diversity would benefit from greater integration of ethnophycology (the study of the relationship between seaweeds and people; see Brodie 2010) on farming practices, and explicit consideration of how farmers perceive cultivar-level variability. Integration of farmer knowledge and their acceptance of research outcomes are essential to produce and utilize new cultivars.

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