

Perspectives on domestication research for sustainable seaweed aquaculture

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1 <u>Title:</u> Perspectives on domestication research for sustainable seaweed aquaculture

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20 Abstract:

In this paper, we address several issues related to seaweed domestication from an 21 22 evolutionary and ecological perspective. We briefly cover the history of human 23 interactions with seaweed and assess the importance of pre-domestication evolutionary 24 processes. The various steps of the trajectory from wild to domesticated seaweed are 25 discussed for five crop seaweeds (i.e. Saccharina japonica (kombu), Pyropia sp. (nori), 26 Undaria pinnatifida (wakame), Gracilaria chilensis (pellilo) and Kappaphycus sp.) to 27 evaluate their domestication status. We show that seaweed domestication resulted from 28 long-term interactions between humans, seaweeds, and environmental factors. This 29 interplay has deeply modified the coastal ecosystem — sometimes with very detrimental effects (pests and invasions) — but was a key element in the evolutionary process leading 30 to domestication. We then highlight the challenges for future research on seaweed 31 32 domestication and show how better integration of knowledge on ecology and genetic diversity of wild populations and on the selective pressures exerted by cultivators canpromote sustainable seaweed aquaculture.

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36 Keywords:

- 37 Domestication, interaction, coevolution, algal resource management, genetic diversity,
- 38 seaweed cultivation and aquaculture, marine agronomy

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42 Introduction

43 Domestication is considered a long and complex process during which domesticators 44 select and modify organisms that can thrive in human eco-environments and express 45 traits of interest for human use (Tanno & Wilcox 2006; Larson et al. 2014). Hence, 46 domestication involves a multi-generational relationship between humans and the target organism. Definitions of domestication vary depending on the nature of this relationship 47 48 and here we adopt the recent definition by Zeder (2015): "a coevolutionary, mutualistic 49 relationship between domesticators and domesticates". Interestingly, Zeder (2015) draws 50 attention to the fact that domestication should be distinguished from resource 51 management and agriculture even if there is a continuum between these three different 52 but overlapping processes. Management is based on the enhancement of the returns of 53 the resource of interest, agriculture is a provisioning systems on the production and 54 consumption of domesticates, whereas domestication is a coevolving mutualism between 55 the manager and the managed resources. This evolutionary approach to domestication focuses on the processes that intensify a species' dependence on humans for 56 reproduction and dispersal (Milla et al. 2015). Moreover, because the evolution of a 57 species leads to evolution of its ecological niche (according to ecological niche 58 construction theory), domestication is also associated with ecological changes in the 59 environment driven by humans to optimize the cultivation conditions of the domesticated 60 61 species (Smith 2016). "This close relationship between humans and their domesticated plants and animals is precisely one of the aspects that makes the study of domestication 62 63 such a fascinating area of study" (Gepts 2010). Full understanding of the domestication 64 process can only be achieved within a cross-disciplinary framework that brings together 65 genetics, evolutionary biology, ecology, and anthropology (Larson et al. 2014, Zeder 2015, McKey et al. 2010) and can provide important insights into general questions in evolution 66 (Darwin 1859, 1868). In addition, research on the pace and biological consequences of 67 domestication is useful for understanding present-day issues of sustainability and 68 69 biodiversity loss (Zeder 2015) and can guide the choices that are made in agriculture/aquaculture systems (Bonneuil et al. 2006). 70

71 The accelerated diversification of seaweed uses in the modern agri-food industry as well 72 as in the pharmaceutical, textile, plastic, biofuel and other industries, is rapidly changing 73 the way we humans interact with this natural resource (Loureiro et al. 2015). In particular, 74 the ever-growing need for raw materials, and the difficulty in sustainably exploiting 75 natural populations, are forcing humans to move from gatherers/fishers to cultivators, 76 and from cultivators to marine agronomists (Buschmann et al. 2014). This latter transition 77 requires a major shift in how scientists, cultivators and farmers, and end-users interact 78 with each other and with the resource. New cultivation processes, adapted from animal 79 and land plant practices, are currently being developed in seaweed aquaculture (Robinson 80 et al. 2013, Hafting et al. 2015), leading humans to influence the fate of natural seaweed populations more and more. However, to what extent human activities have affected 81

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seaweed population evolutionary trajectories has yet to be investigated, because our
 understanding of the on-going domestication processes is only incipient.

In this paper, we first briefly cover the history of human interactions with seaweeds and asses the importance of pre-domestication evolutionary processes. Second, we map the progress of seaweed domestication against the typical milestones that have been identified in land plants and animals, and define what we consider as domesticated seaweeds, referring to the above-mentioned evolutionary and ecological definition of domestication. Lastly, we highlight key questions for future research on seaweed domestication and propose directions for sustainable seaweed aquaculture.

91 History of human interactions with seaweeds

92 Interactions of humans with seaweeds dates back to the Neolithic times (Dillehay et al. 93 2008, Erlandson et al. 2015, Ainis et al. 2014). The most direct evidence of prehistoric 94 human-seaweed interactions comes from the discovery of remnants of 11 seaweed 95 species at the Monte Verde archaeological site in southern Chile (Dillehay et al. 2008). This 96 discovery attests that seaweeds were gathered and consumed for food or medicine at 97 least 14,500 years ago (Dillehay et al. 2008). The earliest written records of human 98 interaction with seaweeds originate from Japan, where wild seaweed consumption was 99 recorded approximately 1500 years ago (Buchholz et al. 2012). According to ancient 100 Chinese manuscripts, Ecklonia kurome growing on the coast of the East China Sea was 101 consumed for its curative effect on goitre more than 1000 years ago (Tseng 1986). Later, 102 Saccharina japonica (also called kombu) growing along the Japanese coast and 103 characterized by much larger populations became the most important source of medicinal 104 seaweed (Tseng 1986). In north-western Europe, brown seaweeds, collected at low tide or 105 as beach wrack (also called varech and goemon), were traditionally employed as fuel, fertilizer and cattle feed but rarely as human food (except Palmaria palmata, also known 106 as dulse) except during famines (in France and Ireland, Arzel 1987). The industrial use of 107 harvested seaweed (mainly kelp) started during the 18th century for soda ash used in the 108 glass-making industry and later for the extraction of iodine and hydrocolloids (Arzel 1987, 109 Forsythe 2006). In Asia, seaweed cultivation for human food began in the 17th century 110 (nori: Pyropia ssp. as Porphyra spp., Wheeler et al. 1979). However, after World War II, 111 112 the chemical industry took over commercial seaweed harvest for the extraction of polysaccharides (Mathieson 1975). The global demand of seaweed products then focused 113 114 on a reduced number of selected species for which natural stocks became insufficient for their supply (e.g. over-exploitation of Gracilaria chilensis in Chile in the 1980s, Buschmann 115 et al. 2008). Encouraged by these demands and in the interest of reducing the over-116 exploitation of natural resources, seaweed cultivation today is practiced around the world 117 (Rebours et al. 2014). All these human practices have likely modified the traits of 118 119 harvested or cultivated seaweeds and the quality of their ecosystems. In light of this brief 120 history, seaweed species and their uses are clearly highly specific to local practices and may have changed with time. Moreover, as for domesticated plants and animals, the 121 management of natural populations and the ease of cultivation may have greatly 122 123 influenced which species were chosen for domestication.

124 The typical milestones on the domestication trajectory

Though domestication is a continuous and dynamic process, common steps have been 125 126 recognized both in plants and animals (Meyer & Purugganan 2012, Larson et al. 2014, 127 Milla et al. 2014 and 2015). This trajectory from wild to domesticated species first begins with humans' deliberate care for wild stands, often called pre-domestication. Population 128 129 management performed to meet human interests, by removing competitors or protecting stands from pests and herbivores, modify the species' environment and therefore the 130 forms and directions of natural selection. Consequently, the target species may evolve 131 132 with regard to several traits related to adaptation to the human-modified environment 133 (Milla et al. 2014), and become increasingly amenable to cultivation. The second milestone is the control of (sexual or asexual) reproduction, a step that requires empirical 134 knowledge of the local species in its environment. An immediate consequence may be a 135 selective shift as humans started to modify (consciously or not) new traits by choosing the 136 137 parental individuals. The third step is the spread of organisms among human ecosystems 138 due to exchanges of biological material, leading to rapid geographical radiation of 139 domesticates. During these early stages, humans exert major evolutionary forces on 140 domesticates by amplifying dispersal and by applying selective forces - consciously or unconsciously — that critically modify the species and its ecosystem. Evolutionary 141 142 divergences emerge between wild and cultivated populations all along these stages. One or several populations of founder gene pools gradually accumulate variable degrees of 143 geographical or genetic isolation from their wild relatives (Figure 1). It is generally thought 144 that this transition lasts several millennia (Smith 1995, Tanno & Willcox 2006) and occurs 145 in different regions (Purugganan & Fuller 2009, Larson et al. 2014). Successive waves of 146 147 plant domestication have been detected: the domestication of most annual crops from 9000 to 4000 BC, followed by most trees from 5000 to 2000 BC, and a third, more 148 contemporary wave of rapid domestication of new crops (e.g. kiwi, cranberry and tropical 149 150 nut trees) (Meyer et al. 2012). Fuelled by the recent burgeoning of aquaculture around 151 the world, involving a wider variety of organisms with a greater diversity of life forms than 152 found in domesticated land species, the current rate of domestication of new species 153 seems to be faster for marine than for terrestrial organisms (Duarte et al. 2007).

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155 An overlooked history of pre-domestication in seaweed

156 One of the first reviews on seaweed domestication focused on the development of breeding programs and genetic improvement of cultivars (van der Meer 1983). Two 157 domesticated taxa, defined as farmed organisms morphologically or genetically 158 differentiated from their wild ancestors as a result of human selection, were recognized: 159 the Rhodophyta Pyropia (as Porphyra sp.) and the Phaeophyceae S. japonica (as Laminaria 160 japonica). Other taxa listed as potentially domesticated were Chondrus crispus, Gigartina 161 162 exasperata, Gracilaria tikvahiae, Kappaphycus (as Eucheuma sp.) because it was possible to select and cultivate fast-growing clones in the laboratory. Based on increased biomass 163 164 production, Duarte et al. (2007) listed 19 marine plants (including seaweeds) as

165 domesticated, all part of the latest, contemporary domestication wave mentioned above. Although Duarte et al. (2007) included seaweeds in their review, the scarcity of relevant 166 publications probably biased their estimation of seaweed domestication success. A critical 167 examination of the 18 seaweed taxa reveals imprecise taxonomic status, suggesting a 168 three-fold over-estimation of the number of species. Most of the scientific publications on 169 170 seaweed domestication postdate the review by Duarte et al. (2007), and were driven by 171 the recent rise in seaweed cultivation (Loureiro et al, 2015). However, the importance of 172 seaweed pre-domestication is generally overlooked, partly because marine seaweeds are 173 highly perishable and rarely survive in archaeological records.

174 Below, we assess the domestication status of five cultivated seaweeds (i.e. S. japonica (Kombu), Pyropia sp. (Nori), Undaria pinnatifida (Wakame), Gracilaria chilensis (Pelillo) 175 and eucheumatoid carrageenophytes (Kappaphycus and Eucheuma spp., Table 1) in the 176 177 light of the domestication trajectory defined above. We focus on evolutionary processes such as artificial selection before cultivation, the interplay between life-history traits and 178 179 domestication, cultivation-induced genetic bottlenecks, genetic and phenotypic 180 differentiation between wild and cultivated populations, the impact of cultivation on the 181 ecosystem as well as signatures of coevolution between human and seaweeds.

182 Importance of artificial selection before cultivation

183 Kombu, wakame and nori all originate from temperate Asia and are used mainly as food for direct human consumption whereas the two others (Pelillo and eucheumatoids) are 184 185 ingredients for the global agri-food industry. Most of these crops show a long history of 186 pre-domestication — dating back from thousands to one hundred years — characterized 187 by the management of wild populations (see references above and Table 1). The 188 importance of artificial selection during this period is difficult to evaluate, yet it is noteworthy that seaweed uses have changed several times (i.e. from medicinal uses to 189 raw products for the chemistry or biochemistry industry, see references above). 190 Therefore, any potential selection exerted by humans in the past likely targeted 191 characters different from the presently selected ones. In contrast, eucheumatoids have no 192 193 history of pre-domestication, since harvesting started in the 1950s (with cultivation 194 beginning in the 1960s) to supply the phycocolloid industry.

195 Impact of life-history traits on the process of domestication

196 The development of massive cultures for seaweed crops was facilitated by the control of 197 their life cycle (either sexual reproduction or vegetative propagation). Wild populations of 198 Gracilaria and eucheumatoids show an isomorphic sexual life cycle with both haploid 199 gametophytes and diploid tetrasporophytes growing from spores. These seaweeds are 200 characterized by a perennial holdfast that naturally produces several fronds, each of 201 which can live independently and propagate vegetatively when detached from the 202 parental thallus. For these seaweeds, cultivation techniques have usually relied only on vegetative propagation techniques although in vitro shedding of carpospores from wild 203 204 plants to generate new "seeds" have been attempted (Buschmann et al. 2001, Luhan & 205 Sollesta 2010, Table 1). The other seaweeds (e.g. Pyropia, Saccharina and Undaria) have 206 heteromorphic life cycles in which a single upright frond grows from the holdfast. For 207 these species, natural populations are maintained by sexual reproduction (i.e. spore production, although asexual spores can be produced in some species such as P. 208 209 haitanensis, Wang et al. 1986). For these species, multi-step cultivation techniques are 210 required to ensure the successful development of each stage of the life cycle in each 211 stage-specific environmental condition (Santelices 1999). Progress in aquaculture initially 212 depended heavily on methods for raising sporelings, such as the one developed in the 213 1950s for Saccharina (Zhang et al. 2007, Table 1). The development of Pyropia cultivation also clearly relied on the understanding and control of the life cycle: the cultivated 214 organism, the macroscopic gametophyte, is based on a microscopic sporophyte (the 215 conchocelis phase; Drew 1949); prior to this publication in 1949, the culture of 216 217 gametophytes relied exclusively on the capture of wild spores (Patwary & van der Meer 218 1992). The control of sexual reproduction eliminates a large amount of uncertainty due to 219 the seasonal fluctuation of natural propagule availability, and allows the development of breeding programmes (for review, see Blouin et al. 2011). In haploid-diploid seaweeds, 220 221 the manipulation of clonal propagation of some life-history stages can facilitate genetic 222 selection. For example, in the brown algae Macrocystis pyrifera, the microscopic 223 gametophytic phase can be cloned and stored as germplasm (Buschmann et al. 2014, 224 Barrento et al. 2016), and repeatedly used in multiple crossing events with varying levels 225 of genetic relatedness.

As in terrestrial plants (Meyer et al. 2012), these cultivated seaweeds are probably 226 characterized by a shift in their reproductive strategy (i.e. from outcrossing to self-227 fertilizing or from sexual reproduction to vegetative propagation) between wild 228 populations and cultivated stands. This differentiation in reproduction is a strong evidence 229 for domestication. The shift from sexual reproduction in the wild to vegetative 230 231 propagation in cultivated farms has been demonstrated for Gracilaria (Guillemin et al. 232 2008) and probably also occurred in Kappaphycus (Ask & Azanza 2002) (Table 1). Clonal 233 propagation enables farmers to selectively multiply superior genotypes and maintain desired phenotypes that would otherwise be lost by recombination during sexual 234 reproduction. In addition, it prevents recombination between selected strains and their 235 wild relatives. Interestingly, unconscious selection during the domestication process 236 237 favoured diploidy in Gracilaria (Guillemin et al. 2008, 2014). Due to its genetic advantage (because heterozygosis only operates in diploids, haploids are hemizygous for all genes), 238 selection for diploidy may be the rule in vegetatively propagated haploid-diploid species 239 (Guillemin et al. 2008, Krueger Hardfield et al. 2016). Clonal propagation has agronomic 240 advantages, such as more rapid growth and greater survival rates (i.e. trade-off between 241 242 fertility, growth and survival, in Gracilaria: Guillemin et al. 2014; in Kappaphycus: Hurtado 243 et al. 2015). Therefore, selection against sexual reproduction is probably strong in 244 vegetatively propagated seaweeds. However, the exclusive use of clonal propagation for 245 crop maintenance, by selecting for sterility, may preclude further breeding improvements 246 (Myles et al. 2011).

In the three sexually reproducing crops, the difference in mating system between natural 247 populations and cultivated stands is poorly documented. These haploid-diploid dioecious 248 species display unisexual male and female gametophytes. In such species, selfing can 249 occur by cross-fertilization between two gametophytes arising from a single sporophyte 250 251 (Krueger Hadfield et al. 2015). Inbreeding and selfing are the predominant mating system 252 in cultivated stands, because of (1) the simplicity of the breeding protocol and (2) the cost 253 of sampling and germplasm maintenance. For example, plantlets depend on germplasm 254 collections based on a limited number of parental individuals in Undaria (Liu et al. 2014), 255 in Saccharina (Zhang et al. 2007, Li et al. 2016) and in Pyropia (Bi et al. 2014) (Table 1). Targeted selection of particular traits (frond length and weight, mannitol, alginate, 256 morphology of the blade and tolerance to higher temperature; Li et al. 2007, Li et al. 2016, 257 258 Zhang et al. 2007) combined with consecutive inbreeding or selfing, gave rise to the first 259 varieties or strains in Saccharina. Little is known, about the importance of selfing in the wild for this species, although population genetics tools are available to examine this 260 261 question (Liu et al. 2012). However, a reduction in productivity of some of these strains 262 has been observed, and has been attributed to inbreeding depression (Liu et al. 2014). Clearly, further studies are required to estimate the effects of a shift in the mating system 263 from outcrossing to selfing. 264

265 **Dispersal outside of their native range for cultivation: consequences on genetic and** 266 **phenotypic diversity**

All cultivated crops have been actively dispersed outside of their native range distribution 267 by humans (Table 1). In vegetatively propagated domesticates, transport over large 268 269 geographic distances has generated extreme bottlenecks during crop foundation. In 270 Gracilaria, reduction in genetic diversity due to a cultivation bottleneck and subsequent 271 clonal propagation has been detected in farms (Guillemin et al. 2008). The cultivation of 272 eucheumatoids now involves 20 tropical countries, often based on small quantities of plants collected in the Philippines (Hurtado et al. 2015). The genetic diversity of cultivars is 273 274 thus probably extremely reduced compared to natural sexual populations (Halling et al. 2013). For crops based on a reduced number of strains, clonality rapidly narrows their 275 276 genetic background and can lead to greater susceptibility to pathogens, as observed for Gracilaria (Leonardi et al. 2006), Pyropia (Kim et al. 2014) and eucheumatoids (Loureiro et 277 278 al. 2015).

279 Such effects of reduced genetic diversity in cultivated stands compared to natural 280 populations has also been reported for some of the three sexually reproducing species (in 281 Saccharina: Liu et al. 2012, Table 1). The case of Undaria is somewhat different since this species has become invasive in introduced areas (Voisin et al. 2005 and references in 282 283 Table 1). A comparison between cultivated Undaria stands and natural (or escaped to the 284 wild) populations within their natural range and in their introduced range shows that genetic diversity depends on introduction history (i.e. single or multiple introductions, 285 Voisin et al. 2005, Table 1). In conclusion, it is clear that the genetic variability of 286 domesticated seaweeds over their natural distribution range has been very poorly 287 explored (Zuccarello et al. 2006, Loureiro et al. 2015, Barrento et al. 2016). Regardless of 288

289 the criteria used to select strains from natural variants, the lack of general knowledge on 290 the environmental and genetic drivers of phenotypic diversity suggests that many other interesting traits may be found in the wild stock. In this context, other domestication 291 strategies are being developed for terrestrial species to both minimize the rate of loss of 292 293 genetic diversity and to encourage local farmers to develop their own local set of cultivars 294 or landraces (Thomas et al. 2011). This approach can be useful for seaweeds that are still 295 mostly managed worldwide by small local fisher communities, such as Kappaphycus 296 (Msuya & Porter 2014) and Gracilaria (Buschmann et al. 2001).

297 Our understanding of phenotypic changes associated with plant domestication and their 298 possible genetic basis comes from a very low number of well-studied crop models that 299 reproduce sexually (Meyer et al. 2012). Nevertheless, due to recombination, artificial 300 selection in sexual species is more complex and slower than in vegetatively propagated species. It is clear from the literature that asexual plant crops encompass a much broader 301 302 range of adaptations than sexual ones (McKey et al. 2010). The evolution of domesticated 303 adaptations can be observed after only a few generations of asexual cultivation (Meyer et 304 al. 2012). When recombination occurs, selection associated with domestication should 305 reduce diversity in some restricted regions of the genome, namely those that contain 306 genes controlling traits of human interest (Wang et al. 1999). Conversely, because clonal reproduction mimics a complete physical linkage over the entire genome, intense 307 selection acting on genes controlling traits of human interest affect the whole genome. 308 309 Interestingly, in their review, McKey et al. (2010) demonstrate that traditional cultivation practices of clonal domesticated plants allow recurrent recruitment of a small amount of 310 sexually produced seeds. These practices thus ensure the maintenance of genotypic 311 312 diversity and the regular reintroduction of recombination. With the methods of next-313 generation sequencing, it is now possible to examine genome-wide patterns of polymorphism to identify genomic regions that show signatures of selection (Beaumont & 314 315 Balding 2004, Nielsen 2005).

316 Impact of cultivation on the ecosystem

317 Intensive farming and domestication are commonly accompanied by profound and often 318 irreversible consequences for the environment. Firstly, the commercial introduction of 319 non-native species or genotypes across continents has resulted in many examples of 320 invasion. Cultivars are usually selected for their tolerance to a large set of environmental 321 conditions and fast growth; once selected for, such all-purpose phenotypes represent a risk for native coastal communities where they can compete with, and sometimes 322 323 outcompete native species (Figure 2). This is the case of Undaria that has proven suitable 324 for cultivation in many different regions, and is now rapidly expanding its range — owing 325 to human-mediated, long-distance transportation - even in regions where it is not 326 cultivated (Voisin et al. 2005, Grulois et al. 2011). Biological invasions may strongly modify 327 native seaweed diversity by direct competition and also by increasing the probability of 328 introducing associated pests. The introduction of seaweeds for aquaculture purposes can 329 introduce new pathogens and act as reservoirs for local ones (see Figure 2).

330 A second risk is through the so-called "crop-to-wild" gene flow, well documented in agriculture (Ellstrand et al. 2003, 2013, Campbell et al. 2006). Importantly, for recently 331 domesticated species, an increase in the rate of domestication leads to an increase in the 332 strength of genetic sweeps and diminishes the reproductive isolation of domesticates with 333 their wild counterparts. This pattern is expected because selective sweeps affect only the 334 335 genomic regions related to the trait conferring the advantage in the new, cultivated 336 environment, whereas the genomic regions determining reproductive isolation are not 337 affected. Such crop-to-wild gene flow can promote the massive spread of the selected alleles, potentially leading to genetic erosion of native populations (Figure 2). In Norway, 338 339 the cumulative introgression of farmed salmon genotypes ranges from 2% to more than 40% in wild populations (Glover et al. 2013). A high level of introgression can thus be 340 observed in some wild Norwegian populations only four decades after farming started. 341 Likewise, hybridization of cultivated seaweeds with native stocks can result in an 342 impoverishment of local genetic diversity, further impacting ecosystem resilience 343 344 (Hutchings & Fraser 2008). However, to date, gene flow from seaweed breeds into native 345 stocks has been virtually unmeasured. The rapid development of fish, shellfish, and crustacean aquaculture over the past few decades further highlights a third risk that needs 346 to be anticipated. For example, the white spot syndrome virus, first discovered in shrimp 347 348 farms in the early 1990s, spread globally in less than a decade and now affects roughly 349 100 wild crustacean species, whose populations may act as reservoirs and vectors (Figure 350 2). In any agricultural or aquaculture system, pests typically reduce production yields by a 351 fifth to a third, a rule that also holds true for cultivated seaweeds (Gachon et al. 2010). 352 Because the use of pesticides is inappropriate [and illegal?] in open sea aquaculture, cultivated stands can also act as a reservoir for pests and pathogens that will further affect 353 354 surrounding natural populations. In all aquaculture sectors, raising awareness of pests and 355 diseases consistently engenders regulations that restrict the movement of broodstock 356 (Stentiford et al. 2010) and imposes rigorous monitoring for symptoms of infectious 357 diseases.

358 Signal of co-evolution between human and domesticated seaweed

359 The long-term domesticate-domesticator interaction eventually leads to mutualistic coevolution (Zeder 2015 and references below). The best-documented examples are the 360 evolution of lactose tolerance in European adults, linked to the appearance of dairy 361 362 products in their diet during the Neolithic (Beja-Pereira et al. 2003) and the increase in the copy number of salivary amylase genes, related to plant domestication (Perry et al. 2007). 363 364 Such co-evolution is likely in progress for seaweeds: a recent comparative gut 365 metagenome analysis revealed that Japanese populations host a bacterium encoding 366 horizontally-acquired porphyranase and algarase, conferring higher digestive ability in this 367 population compared to a control population (Hehemann et al. 2010). Studies of 368 domestication in seaweed may thus bring additional clues on how cultural practices may drive selection in humans. 369

370 Conclusion

371 From the examples discussed above, it appears that domestication resulted from a longterm interaction between humans, seaweeds and environmental factors for species such 372 as Gracilaria (Figure 3), whereas it was only initiated recently for eucheumatoids (Parker 373 et al. 1974). Even if the recent development of aquaculture suggests fast domestication is 374 375 affecting seaweeds, the literature suggests a long history of local practices developed by 376 farmers which probably led to pre-domestication and selection of landraces (Figure 1). 377 Some seaweed crops now depend on humans for their reproduction/propagation, and, 378 likewise, some human social structures depend on seaweed resources. This strong 379 interaction has deeply modified the coastal ecosystem, sometimes leading to very detrimental effects (pests and invasions, Figure 2). Further research on seaweed 380 domestication needs to better integrate these different aspects through multidisciplinary 381 approaches. To conclude, we would like to propose some lines of research on the 382 383 seaweed domestication process that may help the development of sustainable seaweed 384 aquaculture.

385 Understanding which traits and environmental factors are involved in pre-domestication 386 may help breeders and cultivators to select better parental strains for their germplasms, 387 thus optimizing seaweed selection. Furthermore, this selection process may be a cornerstone for the future sustainability of seaweed aquaculture. Ecophysiological 388 experiments on cultivated seaweeds have been conducted for several decades, but should 389 be considered in light of the evolutionary adaptations that can contribute to an efficient 390 391 cultivation system. For instance, the existence of phenotypic plasticity versus local 392 adaptation in shaping the phenotypic variance is largely unexplored, although large phenotypic variance is often reported in association with environmental heterogeneity. 393 394 The actual heritabilities of traits of interest and the genetic correlations between traits or 395 between life stages of the complex, haploid-diploid life cycle are thus far ignored. This raises the importance of developing the quantitative genetics for complex life cycles. 396

The "green revolution" of the mid-20th century provided significant yield improvement 397 (Khush 2001), at the cost of genetic depression of breeds and massive pesticide and 398 fertilizer use. For increased sustainability, new alternative models based on selection of 399 400 local variants aim to maintain the genetic diversity necessary for adapting to future climate risks and meeting food security needs (Fowler & Mooney 1990, Jarvis et al. 2008). 401 402 Because cultivated seaweeds are either wild species or at the very early stages of 403 domestication, the search for a stable, elite phenotype may prove difficult because of the large genetic variance expected in all the traits related to the success of a strain in a 404 405 cultivation system. In addition, it is likely that high spatio-temporal variability hinders the 406 sustainable use of an elite cultivar because the marine environment cannot be 407 manipulated as easily as terrestrial agricultural landscapes are for water, nutrient supply 408 and pest control. Therefore, elite cultivars should be designed only for indoor cultivation 409 systems, whereas the breeding strategy for mariculture systems should take the constraints of environmental variability into account and exploit rather than reduce the 410 genetic variance of specific traits. Molecular-assisted breeding holds much promise to 411 412 mitigate the issue of genetic erosion; acquiring in-depth knowledge on polymorphisms in populations can help identify native genetic genotypes containing desirable traits for "à la 413

414 carte" introgression into local cultivars. Complementary regional efforts to develop full-415 genotype diversity germplasms should be developed to have backup conservation 416 strategies (Barrento et al. 2016).

417 Thirdly, suitable regulations need to be developed to accompany new cultivation 418 endeavours, in accordance with detailed assessments of the potential environmental risks 419 and a clear understanding of conflicting socio-economic interests (Figure 2; Fröcklin et al. 2012). Utmost caution must be applied because of the dispersive characteristics of the 420 marine environment and the lack of reproductive isolation between crop and wild 421 seaweed, for example when considering the potential utilization of transgenesis. Existing 422 423 European and national regulations restrict the release of organisms in the open sea to 424 endemic strains (e.g. European Regulations No. 708/2007, No. 535/2008 and No. 425 506/2008 amending Annex IV to Council Regulation (EC) No. 708/2007). In such environmental assessments, it is also important to foresee that regulations can be 426 427 circumvented, as illustrated by the inadvertent introduction of an invasive alga and viruses 428 alongside illegal introductions of the Pacific oyster in Europe (Mineur et al. 2014), and the 429 illegal cultivation of Kappaphycus alvarezii in northern Brazil (Araujo et al. 2013).

430

In conclusion, research on seaweed domestication should be oriented towards 431 432 management practices and breeding strategies that allow the maintenance of the 433 domesticates' evolutionary potential. This may include the choice of source populations 434 and the selection of varieties suitable for sustainable agricultural systems in the context of 435 spatial and temporal environmental variability, given the difficulty to standardize cultivation conditions in the open sea. Optimization of phenotypic variance (and the 436 437 underlying genetic diversity), rather than minimizing it to homogenize the production, will require a paradigm shift in breeding strategies and a new definition of research goals. 438 439 Ultimately, the dynamic management of seaweed diversity should promote the development of innovative sustainable aquaculture ecosystems that can adapt to the 440 specificities of the marine environment. 441

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- 773 Figure Legends:
- Figure 1: An overview of the domestication process in seaweeds, and the demographic,
- genetic and phenotypic changes involved (modified from Glemin et al. 2009).

A schematic outline of the demographic history of a seaweed crop including a series of nested bottlenecks from wild populations (represented as ovals), and from successive cultivated strands (as rectangles). Gene flow between the seaweed crop and wild populations is indicated with black double-arrows. Both bottleneck and gene flow are integral parts of seaweed domestication history and have opposing effects on genetic diversity. Colours and motifs represent genetic diversity.

a: the first bottleneck corresponding to the cultivation of a few individuals collected from
natural populations and able to grow in a new human-influenced environment; b:
extension of the cultivated genotypes by farming and selection of individuals that present
the best characteristics according to local conditions; c: the second bottleneck
corresponding to the selection of cultivars and varieties from a few cultivated individuals;
d: selection of a mixture of individuals adapted to local farming practices (landraces).

For seaweeds cultivated exclusively through vegetative propagation, i.e. repeated cutting of young branches from the same plant to form 'plantlets' (as performed for *Kappaphycus* and *Gracilaria*), the domestication process can be far more faster and completed in less than 50 years. Further to their domestication, these two seaweeds represent a limited genetic stock (Hurtado et al. 2014, Guillemin et al. 2008).

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Fig. 2. Effect of cultivation on the ecosystem: interaction between wild populations and 794 795 cultivated stands. Three types of biological interactions between wild and cultivated 796 stocks may contribute to the environmental footprint of seaweed domestication: Genetic 797 selection and subsequent crop-to-wild gene flow may affect both allelic frequencies and 798 genetic structure in wild populations. Pathogens can also mediate similar interactions; 799 escapees may also compete with native plants for habitat and reproduction. Therefore, 800 research needs to encompass the development of breeding techniques that maximize 801 yield and biodiversity, the identification and management of pathogens, and the 802 determination of wild genetic resources. For each species, the relative importance of each 803 interaction needs to be assessed, taking into account the biology and life history of the 804 species and the difficulties of biological containment in the marine environment.

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Figure 3: Domestication results from the interactions of seaweed, humans and environmental factors. All three factors are required for domestication to take place (adapted from Gepts 2010).

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Table 1: Domestication stages and main characteristics of seaweed crops.

Creation	Monogon on to finite	Control of convol source duction		Coordination of	Conscience coloction	Unconcelous	Landrasaa	Cultivere	Madification of human	Def
Species	populations	or vegetative propagation for cultivation	Aquaculture: moving individuals from the wild to human ecosystems	Geographical radiation of domesticated species (founder effect, differentiation between wild and cultivated)	(Phenotypic traits)	Unconscious selection (Phenotypic traits, tradeoff)	Landraces	Cultivars	Modification of numan ecosystems (Invasion, pest, gene flow between wild and cultivated populations, decrease of genetic diversity)	Ref
Nori Pyropia tenera (as Porphyra tenera) Pyropia yezoensis (as Porphyra yezoensis) Pyropia haitanensis (as Porphyra haitanensis)	 Harvested and eaten traditionally probably for more than several hundred years in Europe and Asia¹ Proto-aquaculture (as defined by Beveridge and Little 2002) in Asia² 	 Seeding carpospores and conchospores produced by sexual reproduction^{3,4} Archeospore production 	- Cultivation on nets in farms ⁵	-Loss of genetic diversity in farms ⁶	 Fast growth High biomass Tolerance to abiotic stress Synchronization of sexual reproduction Colour Organoleptic qualities⁷ 	- Not studied but probably resistance to desiccation and delay of sexual maturity	?	 Cultivated varieties <i>P. tenera var.</i> <i>tamatsuensis</i> and <i>P. yezoensis f.</i> <i>narawaensis</i>⁸ ZS1: <i>Pyropia haitanensis</i> high temperature cultivar⁵ Germplasm of 500 accessions⁹ 	- Farms suffer from large disease outbreaks and chronic epiphytes ¹⁰	¹ Tseng 1981 ² Miura 1990 ³ Liu et al. 1981 ⁴ Blouin et al. 2011 ⁵ Yan et al. 2005 ⁶ Niwa et al.2009 ⁷ Yan et al. 2010 ⁸ Patwary et Van der Meer 1992 ⁹ Xie et al. 2010 ¹⁰ Kim et al. 2014
Kombu Saccharina japonica	 Harvested and eaten traditionally for probably more than several hundred years in Asia¹¹ 	 Seeding of haploid spores on ropes, production of gametophytes and sporophyte after fertilization¹² Clonal vegetative propagation of gametophytes as a bank of parental strain¹³ 	 Cultivation of microscopic gametophytes in the greenhouse and of sporophytes on floating lines.¹² 	 Introduction of S. japonica in China in 1925¹⁴ Reduced diversity of Chinese cultivars/wild Japanese, Russia and Korean populations probably due to bottlenecks ¹⁵ Loss of genetic diversity in farms ^{15,16} 	 Frond length and weight, mannitol content, alginate content, morphology of the blade and tolerance to higher temperature¹⁵ Organoleptic qualities 	?	- Landraces BN and LZ from China ¹⁵	 Haiqing No1, like 90-1¹⁷ Dongfang No.2 and 3¹⁸ Numerous cultivars^{15,18,19} from interspecific hybrids (901,DF2,DF3) and from intraspecific hybrids (ZK1,ZK2) 	- Low unidirectional gene flow may occur from wild populations to cultivars ¹⁵	 ¹¹ Hurd et al., 2014 ¹² Zhao et al., 2015 ¹³ Li et al, 1999 ¹⁴ Tseng, C.K., 1958. ¹⁵ Liu et al. 2012, ¹⁶Shan et al. 2011 ¹⁷Zhang et al 2007 ¹⁸ Li et al 2007 ¹⁹ Li et al. 2008
<i>Wakame</i> Undaria pinnatifida	 Management of wild populations for probably more than several hundred years in various geographical areas (Japan and China)²⁰ 	 Sexual reproduction and seeding on ropes^{21,22} Clonal vegetative propagation of gametophytes as a bank of parental strain²² 	- Extensive aquaculture in farms close to natural populations in various geographic areas ^{20,22}	- Intentional for cultivation and accidental introduction worldwide ^{22,23,24}	- Fast growing - Organoleptic qualities ⁻²⁵	?	 Different landraces in Japan and in China (different phenotypes)^{26,27} Genetic differentiation between wild/farmed populations and between regions and between native and introduced areas^{25,27,28} 	- Elites?? cultivar (Haibao No. 1 , etc) ²⁹	-Worldwide impact as an invasive species (Red listed) ²⁴ -Escaped from cultivated farms ^{22,29} -Gene flow between wild and cultivated populations ^{23,30,32} - High socio- economic impact ³² - Food ³³	 ²⁰ Sahoo & Yarish, 2005 ²¹ Hwang et al., 2012 ²² Perez et al., 1984 ²³ Grulois et al., 2011 ²⁴ Schaffelke et al., 2006 ²⁵ Saito 1975 ²⁶ Gao et al., 2013 ²⁷ Shibneva et al., 2013 ²⁸ Voisin et al., 2005 ²⁹ Shan (2015) ³⁰ Uwai et al., 1991 ³² Schaffelke & Hewitt, 2007 ³³ Yamanaka & Akiyama 1993
Eucheumatoids Kappaphycus alvarezii (Eucheuma cottonii) Euchema denticulata (as Eucheuma spinosum)	- Originally harvested from natural stocks growing in Indonesia and the Philippines ³⁴	 Cultivation by vegetative propagation using three basic forms: fixed off-bottom, floating long-lines and rafts ³⁵ 	 Aquaculture in farms, fixed off-bottom method usually practiced in shallow reef areas³⁶ 	 Worldwide introduction of <i>K. alvarezii</i> and <i>E. denticulatum</i> over the past 35 years³⁶ Loss of genetic diversity in farms³⁷ 	- Fast growing ³⁶ - Biomass production ³⁶ - Carrageenan quality ³⁴	- Colour varieties ³⁸ - Disease and epiphyte sensitivities	?	 Clonal cultivar: K. alvarezii var tambalang³⁶ Kappaphycus striatum var. sacol³⁹ Large number of strains or varieties (colour, morphotypes)⁴⁰ 	 Positive social and economic impacts on human populations³⁶ ice-ice, a bacterial disease favoured by non-optimal environmental conditions⁴¹; incidence of heavy epiphytism⁴² Introduction in the Solomon Islands, Brazil, Indonesia, Tanzania and the Maldives; generally without any quarantine procedures³⁸ 	 ³⁴ McHugh 2003 ³⁵ Trono 1990; Msuya & Porter 2014; Hurtado et al. 2015 ³⁶ Hayashi et al. 2010 ³⁷ Halling et al. 2013 ³⁸ Ask et al. 2002 ³⁹ Hurtado et al. 2008 ⁴⁰ Trono et al. 2000 ⁴¹ Loureiro et al. 2015 ⁴² Critchley et al. 2004

Gracilaria chilensis	 Proto-aquaculture suggested⁴³ Harvesting natural stock since 1970⁴⁴ 	 Seeding haploid and diploid spores produced by sexual reproduction⁴⁵ Replanting of thallus cuttings by vegetative propagation ⁴⁶ 	 Aquaculture in farms located in sandy/ muddy bays or estuaries, close to wild populations⁴⁷ 	 Extension of the range distribution along the Chilean coast by creation of farms outside of natural range distribution⁴⁸ Loss of genetic diversity in farms ⁴⁹ 	 Fast growing** Biomass production⁴⁶ 	 Selection for diploidy and loss of fertility⁴⁹ Increasing epiphyte load^{46,50,51} 	 Probable landraces from selection of subtidal and intertidal cultivars?⁵² Differences in agar content and susceptibility to epiphytism depending on the geographical origin of strains⁵² Regional genetic differentiation between farms⁴⁹ 	(
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 Diversification of fishing activities⁵¹ Detrimental effect of epiphytism on biomass production^{50, 51} Genetic depletion of both natural and wild populations due to overharvesting and genetic bottlenecks^{43, 49} 	 ⁴³ Guillemin et al. 2014 ⁴⁴ Santelices & Ugarte 1987 ⁴⁵ Buschman et al. 2001 ⁴⁶ Alveal et al. 1997 ⁴⁷ Buschmann & Kuschel 1988 ⁴⁸ Santelices & Doty, 1989 ⁴⁹ Guillemin et al. 2008 ⁵⁰ Kuschel & Buschmann 1991 ⁵¹ Buschmann et al. 1997 ⁵² Buschmann et al.
	1997
	⁵² Buschmann et al.
	1992



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Figure 2.



Figure 3