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1 **A concise review of the brown seaweed *Sargassum thunbergii*—a knowledge**
2 **base to inform large-scale cultivation efforts**

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20

21 **Abstract**

22 *Sargassum thunbergii* is a brown macroalga endemic to the northwest Pacific, playing
23 important ecological roles in structuring and maintaining coastal marine ecosystems.
24 *S. thunbergii* further provides bioactive compounds for potential pharmaceutical and
25 food industries. As food source, it offers high levels of proteins, minerals, and
26 different types of useful amino acids. The present work compiles recently published
27 literature of *S. thunbergii*, with particular focus on the cultivation efforts in China,
28 including breeding of seedlings in the nursery and cultivation at sea. It further
29 presents a concise review of noteworthy applications of this seaweed, its distribution
30 range shifts associated with past climate change, population genetic structure and
31 connectivity, life history, reproduction and development. The compiled knowledge
32 will provide important guidelines for future large-scale farming of *S. thunbergii* that
33 will help to meet the increasing demands of its commercial usage. In turn this will be
34 helpful for the conservation of declining natural populations due to destructive
35 harvesting and rapid ocean changes.

36 **Keywords** Climate change; Cultivation; Ecological adaptation; Genetic diversity;
37 *Sargassum thunbergii*; Phaeophyta

38

39 Introduction

40 *Sargassum thunbergii* (Mertens ex Roth) Kuntze (Basionym: *Fucus thunbergii* Mertens
41 ex Roth) is a perennial marine brown macroalga, belonging to the family
42 Sargassaceae in the order Fucales. It was first described by the German botanist Otto
43 Kuntze in 1880. This species had some homotypic synonyms such as *Cystoseira*
44 *thunbergii* (Mertens ex Roth) C. Agardh 1820, *Myagropsis thunbergii* (Mertens ex Roth)
45 Kützing 1849 and *Turbinaria thunbergii* (Mertens ex Roth) Yendo 1905 (Guiry and
46 Guiry 2021). *Sargassum thunbergii* also had heterotypic synonyms, e.g. *Fucus swartzii*
47 C. Agardh 1815, *Rhodomela swartzii* (C. Agardh) C. Agardh 1824; *Myagropsis swartzii*
48 (C. Agardh) Kützing 1860 and *Sargassum swartzianum* Yendo 1907 (Guiry and Guiry
49 2021).

50 *Sargassum thunbergii* is one of the most common habitat-forming macroalgae with
51 important ecological roles for coastal marine ecosystems. For example, *S. thunbergii*
52 isas can bio-remediate polluted and eutrophic waters by accumulating and degrading
53 heavy metals (e.g., Zn, Cd, Cu and As) (Wu et al. 2010), but also by assimilating
54 nitrogen and phosphorus (Wang et al. 2011).

55 The bioactive components in *S. thunbergii* have many pharmaceutical and
56 nutraceutical applications. For example, an ethanolic extract of *S. thunbergii* inhibits
57 edema without acute toxicity and, thus, presents a potential remedy for
58 inflammation-related symptoms in humans (Kang et al. 2008). Other nutraceutical
59 benefits include the reduction of blood sugar and fat, immune system regulation,
60 elimination of superoxide anion radicals (e.g., $O_2^{\cdot-}$), as well as prevention of thrombus
61 formation and of bacterial infections via functional polysaccharides, polyphenols
62 and/or liposoluble compounds (Sun et al. 2018). Moreover, the extracted alginate,
63 mannitol and iodine are important crude materials for the chemical industry (e.g.,
64 textile production and rubber processing) (He et al. 2011; Sun et al. 2018).

65 Because of its high nutritional value and low alginate content, *S. thunbergii* is
66 widely used in the food industry. This species is rich in protein, vitamin, mineral and
67 umami amino acids. Notably, the macro- and micro-nutrient composition are

68 comparable with the well-known edible kelp *Saccharina japonica* (Areschoug) Lane,
69 Mayes, Druehl et Saunders in East Asia (Table 1) (Tao et al. 2001; Hu et al. 2016).

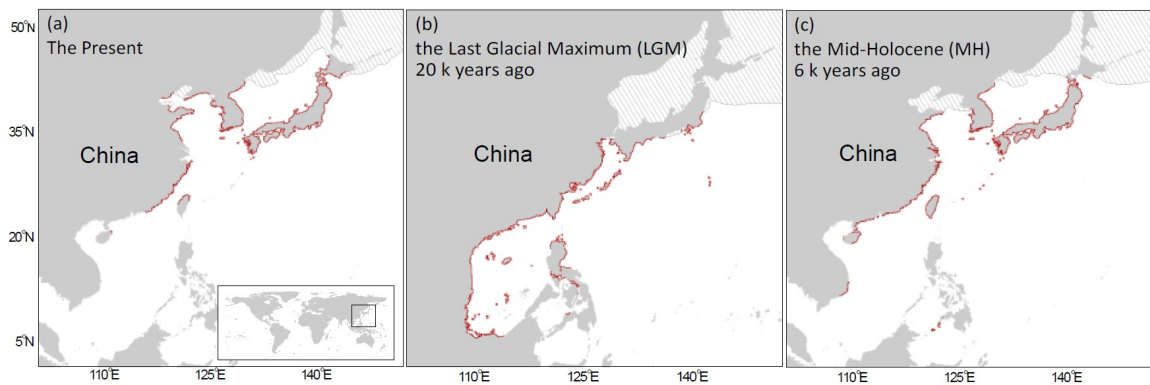
70 Consequently, *S. thunbergii* has a long culinary history in China, Japan and Korea.

71 In Chinese marine aquaculture, *S. thunbergii* was used since the early 2000s as a
72 preferred natural food for sea cucumber and abalone (Han and Li 2005). Juvenile sea
73 cucumber (*Stichopus japonicus*) that had been fed by complementary grinding
74 additives of *S. thunbergii* exhibited a higher growth rate, survival rate and disease
75 resistance than when fed with other marine macroalgae (Zhou et al. 2010; Guo et al.
76 2011). The diverse application potential led to a range-wide over-exploitation of *S.*
77 *thunbergii* in northern China (Liang et al. 2014), and has exerted a considerable
78 pressure to maintain the natural resources. Marine farming of *S. thunbergii* in coastal
79 areas will allow to meet the increasing market and to restore declining populations
80 and the intertidal habitats they support.

81 **Distribution and range shifts driven by historical climate**

82 *Sargassum thunbergii* is one of the most dominant macroalgae endemic to the
83 Northwest Pacific, zoned from mid-intertidal to low supratidal levels. Its
84 geographical range currently spans approximately 25° in latitude from Hokkaido,
85 Japan (44°N) to Hainan Island, China (20°N) (Tseng 1983; Titlyanov et al. 2015). *S.*
86 *thunbergii* currently finds suitable habitat along the coasts of the East China Sea,
87 Yellow-Bohai Bay, the Korean Peninsula and the Japanese Archipelago (Fig. 1a). The
88 distribution range of *S. thunbergii* in the Northwest Pacific has been considerably
89 influenced by historical climate change, particularly the Quasi-100 ky glacial-
90 interglacial cycles triggered by the carbon-climate mechanism, in which climate,
91 carbon cycle and ice sheets interact to produce a feedback that can produce the
92 major observed Quaternary climate variations (Zeng 2006). The periodic, dramatic
93 fall and rise of sea level driven by Paleoclimatic oscillations, re-structured coastal
94 topology and connectivity to surrounding habitats, and hence the distribution of
95 coastal marine sessile species in the Northwest Pacific (Benzie and William 1997).
96 For instance, sea levels in the Northwest Pacific dropped by 120-140 m during the

97 Last Glacial Maximum (20 kya) (Lambeck et al. 2002), leading to the exposure of land
98 mass and the establishment of several marginal sea basins (Fig. 1b) (Wang 1999;
99 Voris 2000). The South China Sea basin became a semi-enclosed marginal sea and the
100 East China Sea basin was reduced to an elongated Okinawa Trough (Fig. 1b). Species
101 distribution models projected a dropped sea level during the Last Glacial Maximum
102 that had considerably shifted the distribution of *S. thunbergii*, with the southernmost
103 boundary of suitable habitats extending approximately to 5°N southward (Fig. 1b). At
104 the same time, the northernmost boundary of *S. thunbergii* was retracted to around
105 35° N (Fig. 1b). When the marginal seas reunited, due to postglacial sea-level rise, *S.*
106 *thunbergii* populations expanded northwards –driven by coastal currents (Li et al.
107 2017). During the Mid-Holocene (6 kya), *S. thunbergii* populations moved eastwards
108 to the coasts of the Chinese marginal seas and northwards to the coasts of the Korean
109 Peninsula and further to Japan (Fig. 1c). Therefore, climate change and associated
110 coastal environmental oscillations have played a significant role in shaping the
111 present day geographical distribution of *S. thunbergii* in the Northwest Pacific.



112

113 Fig. 1

114 **Genetic variation and connectivity of populations**

115 Population genetics provides some of the most crucial information to guide
116 sustainable exploitation and conservation of seaweeds with commercial values. Such
117 information includes genetic population structuring and connectivity, the presence of
118 unique gene pools, pristine habitats and the distribution of genetic diversity within
119 populations. At a regional scale around Shandong Peninsula in China, four *S.*

120 *thunbergii* populations showed high genetic differentiation and a clear relationship
121 between genetic and geographical distances (Isolation by Distance model) (Zhao et
122 al. 2007). Subsequently, two genetic lineages along the coast of China were
123 independently identified by two molecular markers (Li et al. 2017a; Liu et al. 2018).
124 This clear north to south breakage corresponds to the geographic isolation of the
125 low-salinity water lenses in the expansion area of the Changjiang diluted water. In
126 Japan, *S. thunbergii* showed a clear genetic differentiation at SNP loci in double digest
127 restriction site-associated DNA sequencing (ddRAD-seq) between populations from
128 four geographic regions (Kobayashi et al. 2018): Kyushu, the Sea of Japan, Hokkaido
129 and Tohoku, and along the Pacific coast from Kyushu to Kanto. The authors also
130 proposed that *S. thunbergii* populations from Kyushu and the Sea of Japan maintained
131 different genetic lineages from those of China and Korea.

132 Across the entire Northwest Pacific, *S. thunbergii* populations separated into
133 multiple microsatellite-based clusters ($K = 6$, Fig. 2a) with a hierarchical genetic
134 structure (Li et al. 2017b), resembling the phylogeographic structure observed for *S.*
135 *fusiforme* (Hu et al. 2017). This phylogeographic diversity pattern may result from
136 multiple dispersal and vicariance events (Hu et al. 2015; Zhong et al. 2020). *S.*
137 *thunbergii* populations along the Pacific coast of Japan (Pops 1-4 in Fig. 2b) show
138 high levels of genetic variation, which could be explained by the maintenance of
139 distinct ancestral genetic variants (Li et al. 2017b). A deep genetic split was further
140 detected between populations in the Yellow-Bohai Sea (Pops 14-27) and the East
141 China Sea (Pops 28-35) (Fig. 2b). Based on the species' biogeographic history
142 projected by distribution modelling (Fig. 1b, 1c), we can infer that genetic population
143 variation in the Sea of Japan, and along the Korean and Chinese coasts may be
144 explained by vicariance and ad-mixture of populations that have survived the Last
145 Glacial Maximum along the Okinawa Trough and the South China Sea (Fig. 1b; Hu et
146 al. 2017).

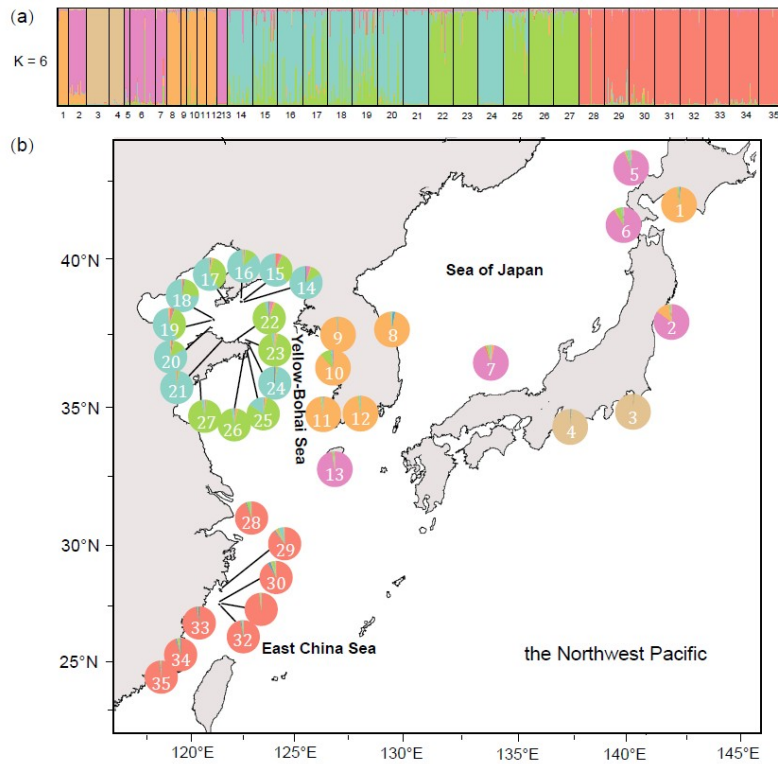
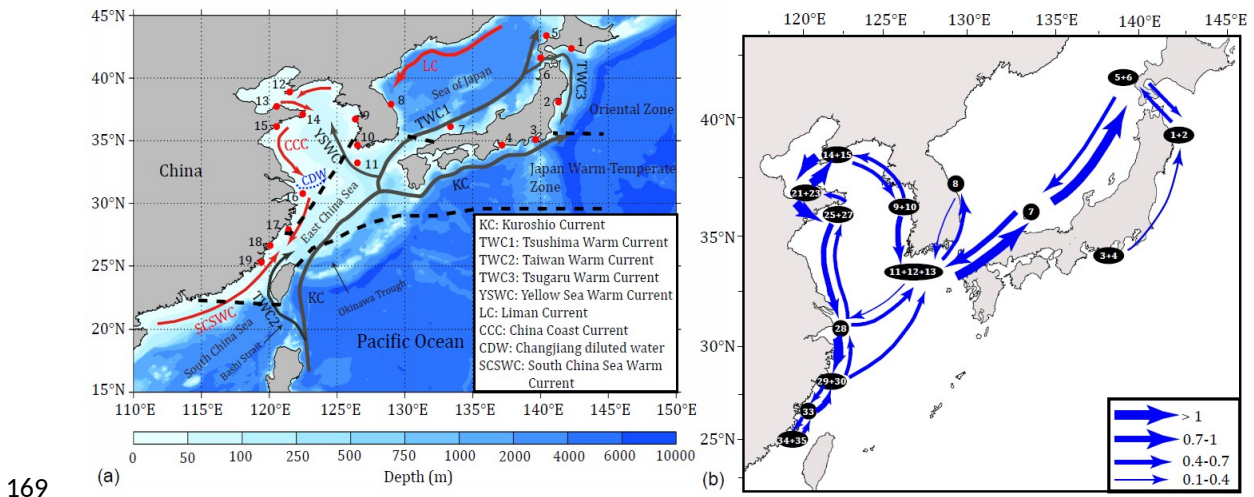


Fig. 2

147

148 Population ad-mixture can be driven by ocean currents. In the Northwest Pacific,
 149 the dominant ocean current system comprises the China Coastal Current, the
 150 Kuroshio Current and its branches (i.e., the Yellow Sea Warm Current, the Tsushima
 151 Warm Current) (Fig. 3a). These coastal currents accelerate genetic exchange between
 152 *S. thunbergii* populations from different marginal seas, leading to ad-mixture of
 153 different ancestral populations. Molecular analyses clearly showed that gene flow
 154 between *S. thunbergii* populations was almost identical to the direction of ocean
 155 currents in this region (Li et al. 2017b). In particular, significant gene flow was
 156 detected from southern China (Pop 28, Pops 29+30) to the Sea of Japan (Pop 7), via
 157 southern Korea (Pops 11+12+13) (Fig. 3b). This suggests that, southern Korea acted
 158 as a transition zone across which *S. thunbergii* populations migrated from the East
 159 China Sea to the Sea of Japan. The Tsushima Warm Current, originating from the
 160 Okinawa Trough, may contribute to genetic connectivity between 2 populations in
 161 southern Korea (Pops 11+12+13) and the Sea of Japan (Fig.3). The dispersal of *S.*
 162 *thunbergii* along the Korean coast appears to be mainly driven by the southward
 163 Korean Coastal Current and northward Tsushima Warm Current (Fig. 3b). Although

164 microsattellites revealed two genetically diverged clusters in *S. thunbergii* along the
 165 coast of China, strong asymmetric gene flow was detected from Pops 25+27 to Pop 28
 166 and from Pop 28 to Pops 29+30, suggesting the China Coastal Current can transport
 167 floating marine organisms (i.e. algal fragments) from the Yellow-Bohai Sea to the East
 168 China Sea (Fig. 3b).



170 Fig. 3

171 **Life history and reproductive characteristics**

172 *Sargassum thunbergii* has a haplobiontic life cycle with the sporophyte as the
 173 dominant diploid phase and the lacks of a gametophyte generation Critchley et al.
 174 1991) (Fig. 4). The gametes are the only haploid phase. The sporophyte of *S.*
 175 *thunbergii* is dioecious, and can reproduce both sexually and vegetatively. Sexual
 176 reproduction in *S. thunbergii* is oogamous. Vegetative reproduction is possible
 177 through rhizoidal extensions, i.e., new thalli germinate around the rhizoid (Fig. 4g).

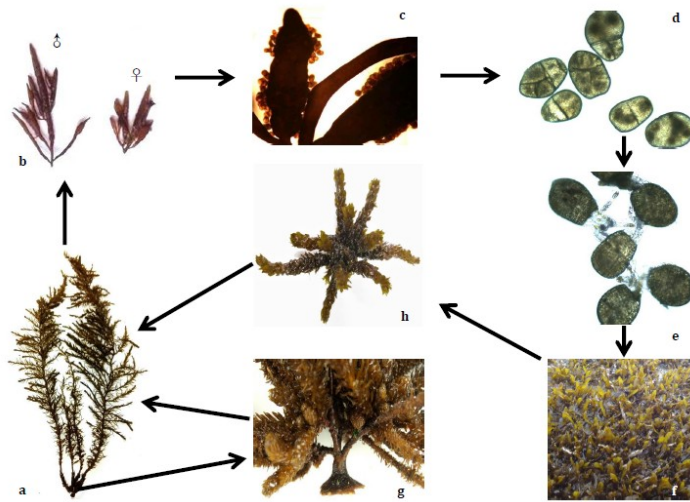


Fig. 4

178

179 *Sexual reproduction*

180 The age of maturity differs among *Sargassum thunbergii* populations from different
 181 sea areas. It increases with latitude and decreasing temperature along the coast of
 182 China. Therefore, it is speculated that sea temperature may be a key factor affecting
 183 the maturation of *S. thunbergii* (Zhan et al. 2006; Wang and Liu 2007; Zhang et al.
 184 2007). When the male and female sporophytes become mature, the receptacles grow
 185 on the specifically modified laterals (secondary lateral branches) (Fig. 4b). The
 186 receptacles are oblong or cylindrical, with a blunt tip. They occur singly or as several
 187 concentrated growing in the leaf (phyllode) axils (Wang et al. 2006). There are
 188 significant differences in shape and size of the receptacles between populations from
 189 different geographic areas. Male and female conceptacles are formed on the male and
 190 female receptacles, in which the antheridia and oogonia develop, respectively.
 191 Generally, the female receptacles are relatively thick and short, about 3-14 mm in
 192 length, whereas the male receptacles are more slender, about 10-23 mm in length
 193 (Wang et al. 2006; Zhan et al. 2006). However, some female and male receptacles are
 194 similar in appearance, and it is not easy to distinguish between sexes when they are
 195 not fully mature (Wang et al. 2006). Following fertilization, a diploid zygote is formed
 196 by the fusion of an antherozoid with an egg, and then germinates immediately and
 197 grows into a new sporophyte (Fig. 4c, 4d, 4e). At the same time, segmentation of the
 198 zygote/germling proceeds rapidly (Critchley et al. 1991).

199 After reaching maturity, the female receptacles are slightly rough due to the newly
200 released eggs or fertilized eggs (zygotes) attached to the surface (Fig. 5a), while the
201 surface of the male receptacles is smooth (Zhan et al. 2006). This phenomenon
202 resembles “incubation” as termed in *S. muticum* (Nicholson et al. 1974). The male and
203 female conceptacles are located within the male and female receptacles, respectively
204 (no self-fertilization). The male conceptacles are relatively sparse, with about 80-120
205 conceptacles on each receptacle, and the diameter of the conceptacle ostiole
206 measures a diameter of about 84-150 μm (Wang et al. 2006; Pan et al. 2007; Wang et
207 al. 2007). The female conceptacles are relatively dense compared to conceptacles on
208 the male, but the total number is smaller than that of male conceptacle, with about
209 60-90 conceptacles on each female receptacle (Wang et al. 2006; Wang et al. 2007).
210 The ostiole of the female conceptacle has a larger diameter of about 130-200 μm . The
211 ostiole diameter in the upper part of the receptacle is slightly smaller than that at the
212 receptacle base, but the conceptacle density in the upper part of the receptacle is
213 greater than that at the receptacle base. The maturity of conceptacles decreases from
214 the base to the top, i.e., acropetal maturation (Wang et al. 2006; Wang et al. 2007).

215 The conceptacle develops from a single superficial cell in the receptacle which is
216 called the conceptacle initial. This cell is flask shaped and larger with a prominent
217 nucleus, making it different from the adjacent cells. The initial cell divides slower
218 than other cells, and, thus invaginates from the adjacent cells. The initial cell divides
219 transversely into two cells, namely the lower basal cell and the upper tongue cell. The
220 tongue cell divides transversely to create a small filament which later disintegrates.
221 The basal cell makes the fertile layer of conceptacles by continuous vertical division
222 (Sun et al. 2007).

223 The cells in the fertile layer of the female conceptacle develop into oogonia (Sun et
224 al. 2007). The oogonial initial cell on the fertile layer of the female conceptacle
225 divides transversely, resulting into a small, lower stalk cell and a large, upper
226 oogonial cell. The oogonial cell enlarges and forms a spherical oogonium. During
227 oogenesis in *S. thunbergii*, meiotic and subsequent mitotic divisions occur without

228 cytokinesis. Therefore, all eight nuclei remain throughout the maturation process of
229 egg. After plasmogamy, one of the eight nuclei fuses with a sperm nucleus and the
230 other seven then degenerate gradually during the development of the zygote
231 (Nagasato et al. 2001; Zhao et al. 2008). This cell forms a single ovum, which will fuse
232 with the nucleus of an antherozoid when fertilization occurs (Pan et al. 2007). The
233 mature oogonia bug out of the conceptacle through the ostiole, but they remain
234 attached to the base of the conceptacle by a long gelatinous stalk. When the oogonia
235 are entirely released from all the conceptacles of a receptacle, the oogonia can
236 completely wrap the surface of the receptacle (Wang et al. 2006; Pan et al. 2007;
237 Wang et al. 2007). This incubation may confer an advantage for *S. thunbergii* to
238 succeed in nursery production (Nicholson et al. 1974). The unfertilized eggs showed
239 strong adhesion ability in an indoor nursery and could detach from the receptacle
240 within nearly 3 days; the fertilized eggs showed weak adhesion and could detach
241 within 1-2 days (Zhan et al. 2006; Wang et al. 2007). Increasing water temperature
242 can stimulate egg release (Zhan et al. 2006). Receptacles of sufficient maturity can be
243 ovulated on the same day – instead of 3-4 days under natural conditions – when
244 placed in a sea water that exceeds temperature in natural conditions by 3-4°C (Zhan
245 et al. 2006; Zhang et al. 2007).

246 The cells on the fertile layer of the male conceptacle can divide transversely to
247 form the lower stalk cells and the upper antheridial cell (Sun et al. 2007). The stalk
248 cells undergo multiple transverse divisions to form more stalk cells and antheridial
249 cells. The antheridial cells enlarge to form spherical antheridia. The diploid nucleus
250 of the antheridial initial undergoes meiosis, followed by repeated mitotic divisions,
251 forming 32-64 haploid nuclei. The nuclei then accumulate cytoplasm and form
252 haploid antherozoids. The antherozoids, pear-shaped with two laterally inserted
253 flagella, are released into the water column after the gelatinization of the outer wall
254 (Sun et al. 2007).

255 *Fertilization and zygote development*

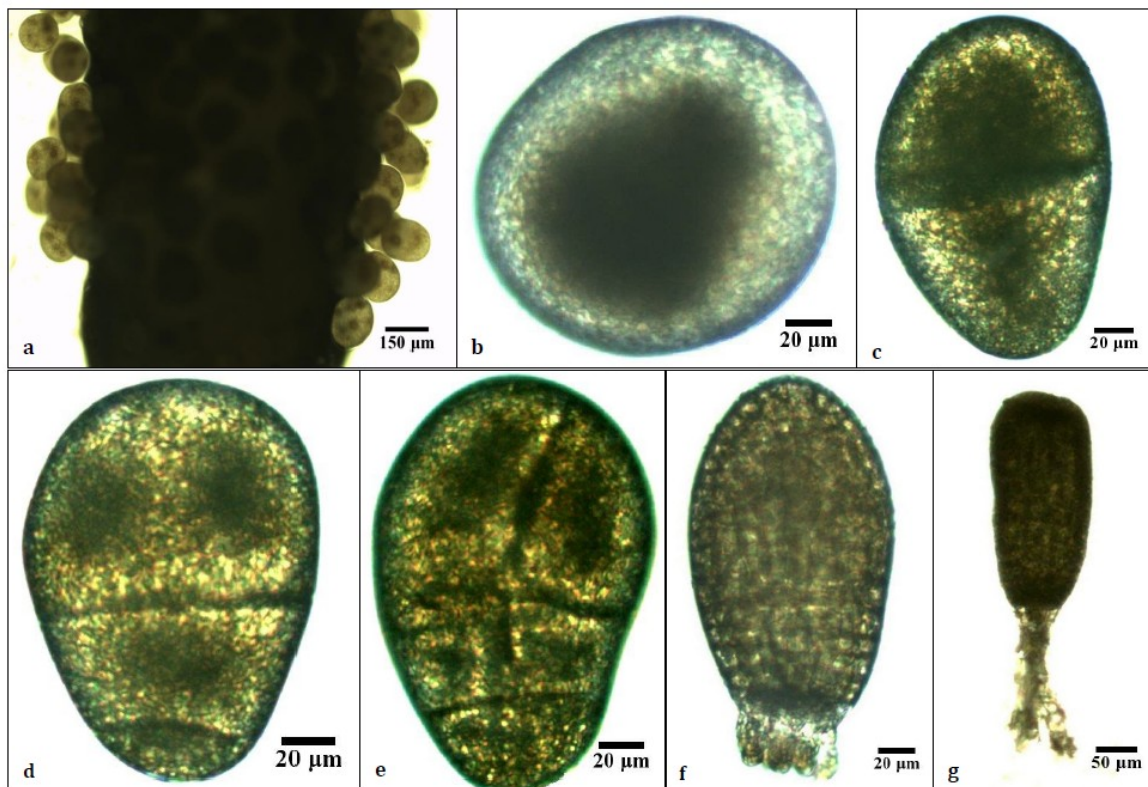
256 In indoor culture of *S. thunbergii*, the ovulation time of the female receptacles is

257 earlier and more concentrated, as compared with the male receptacles (Wang et al.
258 2007). Females can ovulate in the absence of males, whereas the males will often not
259 discharge any antherozoids without females, implying that the antherozoid discharge
260 may be induced by chemical substances released during the ovulation process (Wang
261 et al. 2007). After being discharged from the female conceptacle, the eggs adhere to
262 the outer surface of the receptacle until fertilization (Fig. 5a). After being released,
263 the antherozoids swim to the egg with the help of the flagella and unite with it to
264 form a diploid zygote.

265 About 2-4 hours after fertilization (Liu et al. 2006), the zygote undergoes the first
266 horizontal division to form upper and basal cells, and the basal cell divides again to
267 form a smaller cell at the base, which will further differentiate into rhizoids (Wang et
268 al. 2006; Pan et al 2007; Zhao et al. 2008). The upper cell divides once, approximately
269 every 2-4 hours, and after multiple vertical and horizontal divisions, a pear-shaped
270 embryo sporophyte is formed (Wang et al. 2006; Pan et al 2007; Zhao et al. 2008)
271 (Fig. 5b-5e). When the embryonic sporophyte grows and develops about 16 rows of
272 cells, that is, about 20-48 hours after fertilization, the basal cells form 4-8 protrusions
273 (Fig. 5f), which are the initials of the rhizoids (Wang et al. 2006; Pan et al 2007; Zhao
274 et al. 2008). The protuberances grow continuously, and the rhizoid quickly exceeds
275 the length of the sporophyte thallus (Pan et al 2007).

276 The emergence of the rhizoid indicates the formation of an intact young
277 sporophyte (Fig. 5g), with the ability to attach when falling off from the receptacle.
278 The embryonic sporophyte develops from the fertilized egg within 24-72 hours on
279 the surface of the receptacle, after which it detaches from the receptacle generally
280 from around midnight to the early morning of the next day. Mechanical disturbances,
281 such as agitation, are beneficial to detachment (Sun et al. 2010; Zhang et al. 2007).
282 However, some fertilized eggs or embryonic sporophytes, and even the newly
283 produced rhizoid can remain attached to the surface of the receptacle, and finally
284 detach together with the receptacle from the thallus (Wang et al. 2007). The shed
285 embryonic sporophytes, when attached to a suitable substrate with the rhizoid, can

286 further grow into a large sporophyte.



288 Fig. 5

289 **Seedling breeding in the nursery**

290 In recent years, wild resources of *S. thunbergii* have been drastically depleted due to
291 global climate change and habitat destruction (personal observations), and are, thus,
292 becoming less available for the species' important economic and ecological
293 applications. However, the artificial cultivation of *S. thunbergii* requires a large
294 amount of seedlings, which mainly relied on manual collection from natural
295 populations. As a consequence, the wild resources of *S. thunbergii* have been
296 devastatingly damaged in China. In order to protect the wild resources of *S.*
297 *thunbergii*, an artificial seedling production system has been developed (Fig. 6) (Sun
298 et al. 2007; Li et al. 2009; Zhang et al. 2012).



299

300 Fig. 6

301 *Facilities and equipment for artificial rearing of seedlings*

302 A seedling culture of *S. thunbergii* is generally bred in rectangle concrete ponds at
 303 room temperature (18-23°C) and under natural light (avoiding direct sunlight) (Sun
 304 et al. 2007; Li et al. 2009). In addition to special nurseries targeted to *S. thunbergii*,
 305 nurseries established for other cultured macroalgae can be used, e.g., *Saccharina* spp.
 306 and *Pyropia* spp. (Fig. 6a) Glass greenhouse enclosures need good ventilation, and
 307 glass or transparent Fibre Reinforced Plastic (FRP) should be installed on the roof to
 308 ensure good lighting in the nursery. In the nursery, ponds can be of variable size but
 309 the depth shall not exceed about 0.5 m for optimal operation. In addition, a seawater
 310 treatment system is required, including sedimentation tanks and sand filter facilities.

311 The attachment substratum for the juvenile seedlings of *S. thunbergii* – called the
 312 seedling collector (Fig. 6b) – can be of stones, shells, bamboo, wooden boards,
 313 cement boards, palm-fiber rope (e.g. polyethelene or vinylon) and various fiber
 314 materials (Liu et al. 2017). On account of the efficiency, ease of operation, and cost,
 315 the most commonly used seedling collector is made by weaving vinylon cloth strips

316 (approximately 2 cm in width) onto a plastic frame with a length of 1 m and a width
317 of 0.5 m. This type of seedling collector provides uniform density and firm seedlings
318 attachment, and is convenient to use in practice (Sun et al. 2007; Li et al. 2009).

319 *Selection and treatment of parental thalli*

320 Wild or artificially cultivated populations can be used as parental thalli for artificial
321 rearing of seedlings (Fig. 6c) (Sun et al. 2007; Li et al. 2009; Zhang et al. 2009). The
322 individuals providing best parental thalli are strong and healthy, presenting an
323 abundance of lateral branches and mature receptacles. The level of maturity directly
324 determines the success of seedling breeding (Sun et al. 2007; Li et al. 2009). Upon
325 wrapped by the released eggs, the surface of the female receptacle begins to secrete a
326 large amount of mucus, indicating that the receptacle is ready for seedling collection.
327 Temperature has been proven to be a key factor affecting the maturation of *S.*
328 *thunbergii*. Thus, seasons of growth and production of *S. thunbergii* vary significantly
329 among regions due to temperature differences along the Northwest Pacific coast
330 (Koh et al. 1993; Yatsuya 2008). Therefore, it is necessary to select different locations
331 to collect sufficiently mature individuals at the respective time of the year for
332 artificial rearing of seedlings.

333 *Collection of fertilized eggs*

334 Each square meter of the seedling collector generally needs 0.5-1 kg of parental thalli
335 to provide sufficient propagules, and the weight ratio of female to male parental thalli
336 is about 6-10:1. Before the collection of fertilized eggs, the parental thalli should be
337 rinsed 3-4 times with filtered seawater. It can be dried in the shade for several hours
338 to promote the discharge of eggs. If there are already attached eggs on the receptacle
339 surface, it is not necessary to dry in the shade (Wang et al. 2006; Zhan et al. 2007; Li
340 et al. 2009). There are two methods for fertilized egg collection as outlined below (Li
341 et al. 2009).

342 *Direct collection of fertilized eggs:* The seedling collectors are laid in the nursery
343 ponds sterilized by chlorinated lime, and filled with fresh sand filtrated seawater to a
344 depth of about 30 cm. The parental thalli are laid evenly on the seedling collector, so

345 that the fertilized egg or embryonic sporophyte will fall off naturally and attach to the
346 seedling collector. During the collection, frequent turning the parental thalli can
347 speed up the shedding of the fertilized eggs and facilitates the uniformity of
348 sporophyte attachment. This process will take about 1-2 days, after which the
349 parental thalli are taken out the pond. The fertilized eggs or embryonic sporophytes
350 are not firmly attached at this moment. Thus, during water replacement, water flow
351 must remain slow in order to prevent the sporophytes from being washed away.

352 *Spraying of fertilized eggs:* The parental thalli are concentrated in a nursery pond
353 until the fertilized eggs are shed. The shed eggs and embryonic sporophytes are
354 collected with a 300-mesh sieve, and sprayed onto the seedling collectors according
355 to the planned seedling density (Fig. 6d). Good seedling results have been
356 demonstrated when the density of fertilized eggs is controlled between 8 and 20
357 under the microscope with 100× magnification.

358 *Indoor rearing of seedlings*

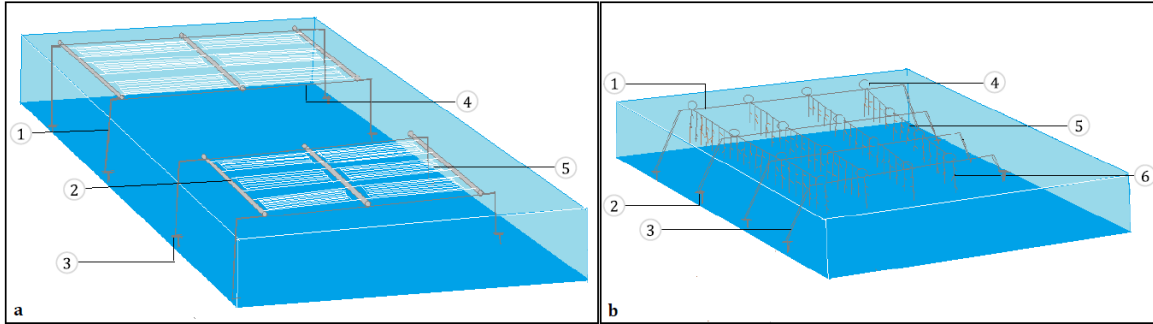
359 Temperature, light and nutrients are important environmental factors affecting the
360 growth of *S. thunbergii* seedlings. Studies have shown that *S. thunbergii* seedlings
361 grow fastest at 18-23°C (Liang et al. 2012; Ma et al. 2013; Wu et al. 2015). The
362 juvenile sporophytes grow well at irradiation ranging from 40-160 μmol
363 $\text{photons}/(\text{m}^2\cdot\text{s})$ (Ma et al. 2013). When the seedlings reach a length of 3-5 mm, the
364 demand for nitrogen increases. At a nitrogen concentration of 2-10 mg/L, the growth
365 rate maintains an upward trend. The optimal phosphorus concentration for the
366 growth of seedlings is 0.4 mg/L, with the optimal ratio of nitrogen-to-phosphorus at
367 20:1 (Ding et al. 2014). *S. thunbergii* seedlings can survive at a salinity of 21-40 PSU,
368 but grow best at 27-30 PSU (Zhan et al. 2006).

369 In the nursery, *S. thunbergii* seedlings are best cultivated with seawater that has
370 been sedimented for 24 hours and filtered through sand. The water temperature is
371 18-23°C, and the sunlight intensity is controlled below 300 $\mu\text{mol photons}/(\text{m}^2\cdot\text{s})$ by
372 window and roof shade. Two or three days after the collection of fertilized eggs,
373 seedling collectors should be washed daily under a gentle water current. After 7 days,

374 the seedling collectors are washed using a pressure water jet with the pressure from
375 weak to strong, regulated to avoid the detachment of the seedlings from collectors.
376 The washing operation should be carried out every other day (Zhan et al. 2006; Li et
377 al. 2009). The washing of seedling collectors is one of the most important tasks for
378 the indoor nursery of *S. thunbergii* seedling. This operation can not only remove
379 other competitive organisms and sludge on the seedling collectors, but also improve
380 the attachment ability of *S. thunbergii* seedlings (Zhan et al. 2006; Li et al. 2009;
381 Zhang et al. 2012).

382 *Seedling transplant from nursery to the sea*

383 After a period of indoor cultivation, the indoor conditions can no longer fully meet
384 the growth requirements of *S. thunbergii* seedlings, and it is necessary to transplant
385 the seedling into the sea (Li et al. 2009). Production practice has shown that if the
386 seedlings are transplanted into the sea too early, the rhizoid of the seedlings remains
387 too weak to support attachment, resulting in the loss of seedlings at sea. However, if
388 the seedlings are transplanted too late into the sea, their growth will be retarded (Li
389 et al. 2009). Rearing practices came to the consensus that the optimal duration for
390 indoor rearing of *S. thunbergii* seedlings takes 10-20 days (Zhang et al. 2007; Li et al.
391 2009). When the seedlings have developed more than 15 rhizoids, and the average
392 thallus height is 2 mm or more, they are ready to be deployed at sea. The seedling
393 collectors are hung horizontally on the floating raft at a water depth of 30 cm (Fig. 7a,
394 Figs. 8a, 8b). After the seedlings had been just transplanted from the nursery, the
395 seedling collectors provide sufficient 'empty' ground for the attachment of various
396 competitive seaweeds, sludge, and invertebrate larvae. If they are not cleaned up in
397 time, the seedlings will be covered, hindered in growth, and can even detach and die
398 (Li et al. 2009; Zhang et al. 2012). Therefore, it is essential to wash the collectors in
399 time – best via the application of high-pressure water jets.



400

401 Fig. 7

402 **Cultivation at sea**

403 Sea areas suitable for the cultivation of *S. thunbergii* should not mix with urban
 404 sewage, industrial sewage, and fresh water from rivers. The water depth at high tide
 405 must exceed 3 m, the current velocity 0.6 m/s, and the salinity 20 PSU. The main
 406 facilities for *S. thunbergii* sea cultivation are floating rafts (Fig. 7b; Figs. 8c, 8d), which
 407 are mainly composed of anchors, anchor ropes, floating ropes, cultivating ropes, and
 408 floats (floating buoys, floating bamboos, etc.).



409

410 Fig. 8

411 When the length of the cultivated seedlings of *S. thunbergii* exceeds 2 cm , the
412 seedlings can be removed from the seedling collector and clamped to the cultivating
413 ropes (Fig. 8d). The distance between seedlings shall be about 8–10 cm. The
414 cultivating ropes should be hanged on the floating rack for cultivation (Fig. 8d), with
415 a space of about 1 m between two ropes. The seedlings then begin to grow rapidly,
416 and form disc-shape rhizoids that can firmly attach to the cultivating ropes. At the
417 end of autumn, several branches sprout from the rhizoid, forming a cluster of thalli.
418 CONTINUE HERE After the fast growing season in autumn, the growth rate of *S.*
419 *thunbergii* slows down due to the low temperature in winter (Chen et al. 2016). In
420 northern China (e.g. Shandong Province), the cultivating ropes need to be lowered to
421 50–100 cm in order to improve the winter survival rate of *S. thunbergii*. In spring, as
422 temperature rises, the growth rates of *S. thunbergii* increases again. From May to
423 June, *S. thunbergii* gradually matures, and is ready to be harvested when the thallus
424 reaches a length of about 2 m (Chen et al. 2016). The daily management of *S.*
425 *thunbergii* cultivation mainly includes: i) inspect the cultivating raft structure to
426 ensure its efficiency and safety; ii) inspect iff seedlings detached and/or got lost due
427 to waves or other reasons– if so, they should be replaced by new seedlings in due
428 time; iii) adjust the water depth of cultivating floats according to the turbidity of sea
429 water.

430 **Prospects for the cultivation of *S. thunbergii***

431 Cultivation on shallow sea rafts can increase the growth rate and, thus, length and
432 fresh weight of *S. thunbergii* by about three times as compared with wild individuals
433 growing on natural rocks (Zhou et al. 2005). Therefore, the increasing commercial
434 demand for this species can best be satisfied via artificial cultivation. The recovery of
435 declining natural populations will have the highest potential when parental thalli
436 originate from cultivated instead of wild grown thalli, and when one seedling is
437 cultivated for 2-3 consecutive years (Yuan et al. 2006) – an exceptional potential of *S.*
438 *thunbergii* because it can regrow vegetatively from rhizoids maintained during the
439 harvest.

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446

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593 **Figure legends**

594 **Fig. 1** Ensemble Species distribution maps for *Sargassum thunbergii* for the present
595 (a), the Last Glacial Maximum (b) and the Mid-Holocene (c).

596 **Fig. 2** Genetic structure of *Sargassum thunbergii* populations based on
597 microsatellites. (a) Each vertical column shows the probabilities (partitioned into
598 sections along the y-axis) of an individual to be assigned to six different genetic
599 clusters that are represented by different colors.(b) Geographic representation of the
600 associated probability of assignments ($K = 6$) for each locality in pie charts. ID
601 numbers for the populations are indicated in the circles.

602 **Fig. 3** The major oceanic current systems in the Northwest Pacific (a) and gene flow
603 estimated between adjacent *Sargassum thunbergii* populations based on 9
604 microsatellites (b).

605 **Fig. 4** The life history of *Sargassum thunbergii*. a: sporophyte; b: mature male and
606 female receptacle; c: eggs on the female receptacles; d: cell division of the zygote; e:
607 embryo sporophyte with rhizoid; f: seedling attached to the substrate; h: young
608 sporophyte; g: new main axis grown from the rhizoid.

609 **Fig. 5** The sexual reproduction of *Sargassum thunbergii*. a: female receptacle with
610 eggs or zygotes; b: fertilized egg; c-e: cell division of the zygote; f-g: embryonic
611 sporophyte with rhizoids.

612 **Fig. 6** Artificial rearing of *Sargassum thunbergii* seedlings in nursery. a: ponds in the
613 nursery; b: seedling collectors; c: parental thalli laid on the seedling collectors; d:
614 samples of young seedlings at different densities attached to the seedling collector.

615 **Fig. 7** Schematic diagram of a floating raft for rearing seedlings (a) and for grown
616 cultivations at sea (b). (a): 1, anchor rope; 2, floating bamboo; 3, anchor; 4, floating
617 rope; 5, seedling collector. (b): 1, floating rope; 2, anchor; 3, anchor rope; 4, floater; 5,
618 cultivating rope; 6, thalli of *S. thunbergii* hung on the cultivating rope.

619 **Fig. 8** Photos of the seedlings (a, b) and cultivations advanced in growth (c, d).

620

621 **Table 1** Proximate composition of *Sargassum thunbergii* in northern China, including
 622 the comparison with the most well-known edible kelp *Saccharina japonica* in East
 623 Asia (after Hu et al. 2016; Cao et al. 2017)

Composition	Content (mg/g dry weight)		Composition	Content (mg/g dry weight)	
	<i>S. thunbergii</i>	<i>S. japonica</i>		<i>S. thunbergii</i>	<i>S. japonica</i>
Protein	142-194	87-162	Asp [*]	11.3-14.8	19.8
Crude fat	1.700-60	2.000-15.400	Ser [*]	4.9-6.0	2.78
Carbohydrate	590-656		Glu [*]	31.1-43.9	28.7
Crude fiber	44	98	Gly [*]	5.0-7.5	3.14
Vitamin C	0.206	0.110	Ala [*]	6.5-13.3	4.81
Ca	2.600	2.900	ΣUAA	71.2-74.8	59.19
K	30.600	42.700	EAA	32.7-58.8	15.98
P	1.100	1.900	HEAA	6.4-10.2	4.22
Sr	0.885	0.340	TAA	135.4-145.8	80.01
Zn	0.028	0.013	ΣSFAs (%)	29.91-36.00	43.76
Cu	0.014	0.007	ΣMUFAs (%)	18.33-24.78	25.00
Mn	0.077	0.012	ΣPUFAs (%)	29.42-41.77	20.69

624 ^{*}UAA, umami amino acids; EAA, essential amino acids; HEAA, half-essential amino acids; TAA,
 625 total amino acids; SFAs, saturated free fatty acids; monounsaturated fatty acids; PUFAs,
 626 polyunsaturated fatty acids