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Mariculture of the Asian kelp *Undaria pinnatifida* and the native kelp *Saccharina latissima* along the Atlantic coast of southern Europe: an overview

Running title: Mariculture of kelps in southern Europe

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Abstract

Kelps are one of the most economically and ecologically important groups of seaweeds in the world. Most kelps are confined to cold temperate regions, and northern Spain is the southern distribution limit of many species in Europe. As the supply from wild harvest cannot meet increasing current and future demands, methods to successfully cultivate kelp species are needed. This review integrates key points about mariculture of kelp species from different cultivation trials conducted along the Atlantic coast of southern Europe, and more specifically about *Undaria pinnatifida* (wakame) and *Saccharina latissima* (sugar kombu) along the northern Spanish coast. It focuses on the following topics: (1) effects of hydrodynamic conditions on culture grounds in coastal bays in order to identify optimal locations for culture of both kelp species; (2) suitability of different raft culture systems in sheltered and more exposed environments; (3) identification of the most suitable time frame for the mariculture of both kelps and its relationship with environmental factors; and (4) different methods for open-sea cultivation of *S. latissima* based on practices traditionally employed in Asian *Saccharina* farming. Finally, (5) this paper discusses the development of mariculture of the introduced kelp, *U. pinnatifida*, in relation to the native kelp, *S. latissima*, both from economic and environmental perspectives. Overall, the information reported here contributes to the knowledge necessary for the successful mariculture of these and other kelps on a commercial basis in this and other areas of Europe.

Key words: kelp mariculture, *Saccharina latissima*, Southern Europe, Spanish experiences, *Undaria pinnatifida*

1. Introduction

Kelps constitute an economically and ecologically important group of seaweeds that are used mainly as human food and as a source of alginate for a wide range of industries (textile, food, paper, cosmetic, and pharmaceutical). However, kelps also have many other commercial applications, such as feed for aquaculture and animal husbandry, agricultural fertilizers, feedstock for biofuel production, and medicinal purposes [1, 2]. In addition, these large algae play important roles as ecosystem engineers and/or foundation species (kelp forest), providing habitat, protection, and food for numerous organisms in coastal ecosystems [3, 4].

The commercial kelps *Undaria* (wakame) and *Saccharina* (kombu) were traditionally collected in eastern Asia from wild stocks, but this practice has been replaced to a great extent by mariculture. World aquaculture production of wakame and kombu currently accounts for more than 95% of total production [2, 5]. In contrast to Asia, kelp species in Europe are still wild harvested for industrial purposes, although natural resources are limited [1, 2] and populations have declined in recent years due to climate change [6-8]. Mariculture of kelp species has generated great interest in recent years, as it may lead to increased production for commercial uses and potential applications in integrated multitrophic aquaculture (IMTA); in turn, it may help protect the kelp forest from overharvesting [9-12].

Most kelps are confined to northern temperate regions with relatively cold water, and the Iberian Peninsula (northern Spain and Portugal) represents the southern distribution limit of many species in Europe [13]. The introduced kelp *Undaria pinnatifida* (wakame) and the native kelp *Saccharina latissima* (sugar kombu) are two of the most valuable seaweeds in northern Spain due to their high demand and economic value. The retail prices of wakame and sugar kombu are approximately 61−66 and 40−49 euros per kg dry weight of useful blade, respectively, in markets whose goods are intended for human consumption, which is their principal use today [14]. As the supply from wild harvest cannot meet increasing current and future demands, mariculture of these kelp species is currently a growing enterprise.

The purpose of this paper is to review kelp mariculture based on experience gained and research developed from commercial-scale cultivation trials along the Atlantic coast of northern Spain. This review focuses on describing the following: (1) the effects of hydrodynamic conditions on kelp culture grounds in coastal bays to identify optimal locations for the cultivation of *Undaria pinnatifida* and *Saccharina latissima*, (2) the suitability of different floating rafts equipped with culture systems built using horizontal rope (long-line) or hanging rope (garland and vertical types) in sheltered and more exposed environments, (3) the identification of the most suitable time frame (outplanting and harvesting period) for the mariculture of both kelp species along the Atlantic coast of southern Europe (northern Spain) and the relationship of the time frame with environmental factors, and (4) the different methods of open-sea cultivation tested with *S. latissima* based on practices traditionally employed for the Asian

Saccharina japonica (two-year cultivation, forced cultivation, cultivation by transplanting). Finally, this paper also discusses (5) the development of the mariculture of the introduced kelp, *U. pinnatifida*, in relation to the native kelp, *S. latissima*, from economic and environmental perspectives, taking into account the potential risks and/or benefits associated with the cultivation of these species. Overall, this review provides insights applicable to development and implementation of open-sea cultivation of kelps species on a commercial basis along the southern Atlantic coast and other areas of Europe. In particular, this review provides baseline information required for the successful mariculture of *U. pinnatifida* and *S. latissima* on the northern Spanish coast.

2. Methods and data sources

Gametophyte stock cultures (germplasm collection) from the Spanish Institute of Oceanography (IEO) in Santander were used to produce seedlings of *U. pinnatifida* and *S. latissima*. These gametophyte cultures were derived from zoospores released from sporophytes cultivated in Galicia and along the Cantabrian coast of Spain (Northern Spain). The original parents were collected from wild populations of *U. pinnatifida* in Gijón (Asturias) in 1996 and Lorbe (Galicia) in 2001 or from natural populations of *S. latissima* in Cambados (Galicia) in 1996 and Oleiros (Galicia) in 2001. The sporophytes originating from Iberian populations have been actively bred by successive inbreeding and directional selection since 1996, in order to obtain cultivars or strains with strong growth, high-quality morphological traits and high tolerance to high temperature [15]. Note that the Asian kelp *U. pinnatifida* was accidentally introduced in Spain on the Atlantic coast of Galicia in 1988 and that it has spread widely since then [16]. Spore suspensions and gametophyte cultures were obtained using the methodology developed by Perez et al. [17, 18]. Seedlings attached to strings were produced from crossing of gametophytic clones of the IEO collection with high similarity according to the protocols described in previous studies [9, 19].

Open-sea cultivation trials for *U. pinnatifida* and *S. latissima* were conducted at two different locations in an enclosed coastal bay off A Coruña, (Galicia), and trials were also conducted for *S. latissima* in an open-sea coastal region off Santander (Cantabria); all sites lie off the Atlantic coast of northern Spain. The farms in Galicia consist of a sheltered site and a moderately exposed site with current velocities no greater than 12 cm s^{-1} and 27 cm s^{-1}, respectively [20, 21]. The farm in Cantabria is an exposed site with currents ranging from 48 to 92 cm s^{-1} [22]. Pilot-scale floating rafts with horizontal ropes (long-line) or hanging ropes (garland and vertical types) were used for cultivation trials in the sea (summarized in Figure 1).

The information presented here integrates and summarizes results gained from different culturing experiments carried out at a pilot scale at these farm sites [9, 19, 23-31]. The summarized data of cultivation trials with *U. pinnatifida* and *S. latissima* along the northern Spanish coast are presented in Supplementary Tables 1 and 2

(Appendix A. Supplementary data). These tables contain the following information (if available): references; cultured kelp, localities along the Atlantic coast of northern Spain, wave exposure and/or water velocity at the culture site, seed type used for the cultivation (seedling or frond transplantation), rope culture type (vertical rope culture, garland rope culture or horizontal rope culture), culture depth, anchor systems of floating raft (fixed to concrete blocks vs. poles), outplanting date, harvesting date, production cycle (1-year or 2-year production cycle), mean yield per length rope, mean length of fronds, mean fresh weight of fronds and absolute growth rate (on the basis of length and/or weight change of cultured fronds).

In addition to determining the key environmental factors that are related to the timing of cultivation of *U. pinnatifida* and *S. latissima* off of the Atlantic coast of southern Europe (northern Spain), this paper examines seawater temperature, dissolved inorganic nitrogen, underwater irradiance and day length during the most suitable culture time frames using data recorded by INTECMAR at a farm site of Ría de Ares y Betanzos in Galicia (northern Spain) ([32, 33]; http://www.intecmar.org/).

3. Hydrodynamic conditions for cultivation

3.1 Determining the quantity and quality of the yield

The hydrodynamic conditions at the farm site markedly affected the cultivation of *Undaria pinnatifida*, with a significantly higher biomass yield (an approximately twofold increase in yield) and larger frond dimensions (i.e., blade weight and blade area) at the most exposed site in Galicia (northern Spain) [19]. These morphological characteristics of the frond were related to the quality of the frond as a product marketed for human consumption. Thus, the hydrodynamic environment appears to represent a key factor controlling the production and quality of *U. pinnatifida* in mariculture. However, for the trials with *Saccharina latissima* at the same sites, the hydrodynamic conditions at the moderately exposed site had a weak positive effect on the biomass yield, although this yield did not differ very significantly from that at the sheltered site (the yield values differed by 25% between the locations). These differences in yield between the two culture sites of *S. latissima* may be explained by the contrasting levels of water movement as well as light exposure, which is also indirectly related to the degree of water motion [29]. Hence, the lower amount of light at the more sheltered site likely has a much more pronounced effect when combined with low light-use efficiency because the amount of water movement is less than the amount at the moderately exposed site [34, 35]. In contrast, significant differences between sites in some morphological characteristics of *S. latissima* (frond length, frond weight, blade length, blade area, and blade weight) were observed. However, the "substantiality values" (i.e., the index values used to assess the quality of kombu for human consumption based on the characteristics of the leaf blade [36, 37]) were similar between sites. The “substantiality value” of the blades (mg cm^{-}

^{2}) of *S. latissima* is directly correlated with the blade thickness of the cultured sporophytes, and the thickening stage occurs primarily during the summer [27], as described by Parke [38] in natural populations. Therefore, the lack of difference in substantiality values between the two culture sites is consistent with the timing of the cultivation trials (which were conducted exclusively in late April). However, the patterns of morphological variation (e.g., blade width and stipe length) that are associated with the hydrodynamic regime in *S. latissima* [38, 39] and other kelps [40, 41] were not observed.

The observed differences between the kelp species in the effects of hydrodynamic conditions on the quantity and quality of yield have several potential explanations. These explanations are presented for the first time here to integrate the study results presented above. First, the high sporophyte density obtained through *S. latissima* cultivation (500−700 sporophytes m^{-1} rope) in our experiments almost certainly decreased the effects due to water movement. This is not the case for *U. pinnatifida* cultivation, which results in a low sporophyte density (60−100 sporophytes m^{-1} rope). Many studies have indicated that a high density of individuals in a restricted space (e.g., on a culture rope) can limit the impact of the hydrodynamic environment and light exposure on the fronds [42-45]. Second, these differences may reflect different requirements or different responses to water movement. The effects of water velocity may vary among seaweeds, as observed in other studies [46-50]; such variation reflects differences in ecophysiological and/or morphological traits. In marked contrast to the perennial kelp *S. latissima*, the annual kelp *U. pinnatifida* shows a high level of metabolic activity and, in turn, exhibits poor nutrient uptake at low concentrations; it also displays low internal nitrogen reserves [51-54]. Thus, *U. pinnatifida* is almost certain to benefit strongly from the increased water motion, which has been shown to enhance nutrient uptake in kelp species [55-57]. Recent field experiments have demonstrated that the up-and-down leaf movement produced by the motion of water across the ruffles or undulations of *S. latissima*'s blades significantly enhances nutrient fluxes to the blade surface at a low current velocity. However, this effect is not as marked in the presence of a high-velocity current. Thus, such up-and-down motion is more beneficial for nutrient uptake at sheltered sites than at exposed sites [58]. This observation could explain why this species is most commonly found in locations with a weak to moderate current [38, 59, 60].

In applications, water movement is a key factor affecting yield quantity and quality either directly or indirectly; thus, it should be considered in determining the optimal locations for kelp mariculture. Water movement is a key determinant of seaweed production: it directly influences the uptake of nutrients and carbon dioxide and indirectly influences most factors affecting growth [41, 61, 62]. Moreover, variations in kelp morphology associated with differences in hydrodynamic regimes are well known [41, 63], and blade morphology has significant implications for assessing the quality of edible kelps [36, 64].

Specifically, the results of the present review showed that *U. pinnatifida* cultivation was more successful at a moderately exposed site with seawater velocities of up to 27 cm s^{-1} than at a sheltered site with low seawater velocities of up to 12 cm s^{-1}. These data are consistent with the findings of a similar, previous study conducted in the Okirai Bay of Japan, in which seawater velocities ranged between 5 and 15 cm s^{-1} [65]. In nature, *U. pinnatifida* also shows a clear preference for habitats with pronounced water movement. This species usually occurs on exposed shores or within bays in locations near the open sea [66-69]. In contrast, *S. latissima* cultivation was suitable for both sites (sheltered and exposed), where the seawater velocities ranged from 12 to 92 cm s^{-1}. This species has also been cultured on offshore wind farms in the German North Sea under rough conditions where the current velocity was greater than 200 cm s^{-1} [70, 71]. However, *S. latissima* is most commonly found in habitats with low to moderate water movement [38, 59, 60].

3.2. Suitability of different raft culture systems

Various raft systems using horizontal ropes (long-line) and hanging ropes (garland and vertical types) with some introduced modifications (summarized in Figure 1) were tested at both a sheltered site and a moderately exposed site in a coastal bay (ría) of Galicia (northern Spain) [19, 24, 26-29]. These culture rafts were similar to others employed commercially in Asian waters [36, 72] and have been tested experimentally in western countries [17, 70, 73-76]. A new type of anchoring system was also evaluated at an exposed site off the Cantabria coast (northern Spain). This site is fully exposed to ocean swells. The new system was supported on poles fixed to the sea bottom [9]. Under these conditions of high exposure to wave action and other water movements, the concrete blocks traditionally employed to securely moor the floating rafts are washed ashore by storms, as observed in previous cultivation trials at this location. Little is known about the suitability of different culture raft systems in sheltered environments or at more exposed sites [70].

This review shows that at sheltered sites with low current speeds of up to 12 cm s^{-1}, hanging rope culture provides better water motion than horizontal rope culture because the hanging rope culture more easily maintains an appropriate degree of tension that favours the flow of water over the kelp and thereby increases the uptake of nutrients by reducing diffusion across the boundary layer. As Neushul et al. [77] demonstrated, a culture rope under tension produces greater water velocity than a rope without tension. However, hanging culture resists high levels of water movement, which can lead to rope tangling, damaging the culture. In contrast, horizontal ropes (long-line) are much more resistant to water movement, as suggested by previous descriptions of kelp cultivation in Asia [72, 78]. Thus, horizontal ropes are more suitable for kelp mariculture in environments with moderate to high degrees of water motion, with speeds ranging from 27 to 92 cm s^{-1}.

The assembly and harvest of hanging rope culture is easy relative to those of rope horizontal culture. The most important disadvantage of hanging rope culture (garland and vertical types) is the lack of light uniformity along the culture rope due to depth differences and the shadow effect of the seaweeds. However, garland hanging rope exhibits more gradual decreases in depth along the rope, thereby minimizing the shadow effect of the seaweeds relative to vertical hanging rope. Regardless of the hanging rope type, to minimize the disadvantage of non-uniform light levels, it is necessary to position the lengths of rope within an optimal depth range. The optimal biomass yield in the farms sites of Galicia typically occurred at a culture depth of 0–2 m for both *U. pinnatifida* and *S. latissima* (light saturation levels are greater near this depth range, see Figures 5 and 6), although the actual optimal depth for cultivation may vary among culture seasons and sites depending upon the transparency and turbidity of the water [9, 24, 25, 29, 76].

The reliability of the fixed-pole anchor system for culture rafts has been successfully demonstrated at open-ocean sites with a high level of water motion (i.e., up to 92 cm s^{-1}). Other studies have also successfully tested different systems for open-ocean kelp aquaculture. For example, a system in use on offshore wind farms under open North Sea conditions has been designed and tested with *S. latissima* under very rough conditions with current velocities greater than 200 cm s^{-1}. The horizontal and hanging rope cultures were considered unsuitable for kelp mariculture in these more exposed sites of offshore wind farms [70]. In contrast, in cultivation trials in Galicia (Northern Spain), culture rafts attached to concrete blocks have been shown to be well suited for coastal areas of sheltered bays with current velocities no greater than 27 cm s^{-1}. This approach has been used successfully in kelp farming in both Asia and the West [17, 36, 72, 74-76].

4. Time frames for cultivation

4.1. Outplanting and harvesting time

On the basis of the cultivation trials detailed in this study, the most suitable outplanting dates for *U. pinnatifida* and *S. latissima* appear to be October to November and November to December, respectively, and the crop should be harvested from March to April and from April to May, respectively [9, 19, 24, 26-29]. These and other major seasonal stages for the mariculture of these kelps on the Atlantic coast of southern Europe (northern Spain) are summarized diagrammatically in the schedule shown in Figure 2. The culture time frame for *U. pinnatifida* suggested by the current experiments (Figure 2A) is similar to the one used for traditional farming in temperate Japanese waters (i.e., outplanting in September to November, final harvesting between March and May), but marked differences are evident between this time frame and the time frame used previously in cold Japanese waters (i.e., outplanting in August to January and multiple partial harvests between May and July) [66, 68, 72]. Nevertheless, it is important to emphasize that under current cultivation practices, *U. pinnatifida* is mainly outplanted from September to October and harvested from February to April (information from Japanese farmers provided by an anonymous reviewer) (see Figure 3; this schedule summarizes the time frames for the outplanting and harvesting periods for the traditional and current mariculture of *U. pinnatifida* in Japan). In this Asian region, the time frame for mariculture is well defined because *U. pinnatifida* is native to these waters and has been traditionally farmed, and the seawater temperature is considered one determining factor for the choice of optimal outplanting and harvesting dates [64, 66, 79, 80]. The seasonality of *U. pinnatifida* cultivation in European Atlantic waters may be related to a lower level of fluctuation in seawater temperature compared with the level in the species' native Asian waters. This difference may explain the difference in seasonal growth between European Atlantic populations and Asian populations of *U. pinnatifida* [81-83]. The previous attempts to cultivate this species on the Atlantic coast of Galicia have also shown a culture time frame (i.e., outplanting in October to December and final harvesting between February and March) [76] similar to the one described here. The observed differences in the outplanting and harvesting periods between our trials and the studies reported to date in other locations of Galicia are most likely due to slight local differences in environmental factors (e.g., dissolved inorganic nitrogen and hydrodynamic conditions). Hence, the outplanting and harvesting dates may be a month behind or ahead within a limited geographical region; thus, testing a farm site and identifying the environmental conditions are very important for adequately defining the appropriate culture time frame. Regardless, knowledge of the key environmental factors related to the timing of cultivation (i.e., the beginning and end of culture in the sea) outside Asian waters remains very limited; this issue has not yet been explored in cultivation trials in European waters [17, 19, 23, 24, 76].

The time frame that is best suited for *S. latissima* mariculture may differ among areas or regions. For example, important differences exist between the most desirable culture period identified by the current study (Figure 2B) and the best culture period found by previous cultivation trials performed in coastal waters of the United Kingdom [74, 84, 85]. However, prior to the current study, the most suitable outplanting and harvesting period for the mariculture of this kelp species at the southern limit of its distribution in European waters was unknown, and the key environmental factors related to the timing of cultivation in this region were also unknown. Thus, there was a need to determine the best time frame for the cultivation of *S. latissima* to define an optimal approach to the mariculture of this species along the Atlantic coast of northern Spain. In previous studies of cultivation in United Kingdom waters, the sporophytes outplanted in December and February were very similar in length and weight and were much larger than those obtained from earlier outplantings in November or later outplantings in April [74, 84, 85]. This disparity in the preferred times for the initiation of cultivation in the sea is most likely related to differences in environmental conditions along a latitudinal gradient, as *S. latissima* in northern Spain is at the southern limit of its distribution, whereas, in the United Kingdom, it is in the middle of its geographical range [13, 86]. It is likely that temperature differences are the principal basis of the observed differences among areas in the best time frames for culture. Temperature is considered one of the key factors that induce latitudinal changes in the growth patterns and phenology of kelp species because it decreases as latitude increases [1, 87]. Therefore, populations of *S. latissima* in the cooler waters of higher latitudes have a longer growing season as well as perennial sporophytes that persist through the summer temperatures and that have a longevity that can exceed 3 years [38]. In contrast, southern populations have a shorter growing season, with sporophytes decaying or disappearing in early summer; they can be annual in many cases due to the warm water temperatures experienced during the summer [27, 88]. Consequently, this kelp species is confined to northern temperate regions with cold water, usually below 20°C, and the southern limit of its distribution is the northern Iberian Peninsula [13, 27, 86]. The best outplanting time period for the mariculture of *S. latissima* along the Atlantic coast of southern Europe (northern Spain) is similar to that used for commercial farming of *S. japonica* in Asian waters using the "forced cultivation" method (i.e., the culture period in the sea is reduced with outplanting from October, see Figure 4 for more details) [36, 37, 78, 89, 90]. This is consistent with the results of recent trials with outplanting in November in Galicia, northern Spain [31].

4.2. Key environmental factors affecting cultivation

As mentioned above, this review examined seawater temperature, dissolved inorganic nitrogen, underwater irradiance and day length in Galicia (northern Spain) during the most suitable culture time frames to determine the key environmental factors related to the timing of the cultivation of *U. pinnatifida* and *S. latissima* along the Atlantic coast of southern Europe. Figures 5 and 6 show the possible influences of environmental factors on the time frames for the outplanting and harvesting period for the mariculture of both kelps. The outplanting time for *U. pinnatifida* mariculture coincided with decreases in temperature (approximately from 17 to 14°C), irradiance (levels falling below 150 μmol m^{-2} s^{-1}) and photoperiod (less than 12 h of light per day), whereas the dissolved inorganic nitrogen increased (to 5−10 μM). In contrast, the harvesting time coincided with increases in temperature (above 15°C), irradiance (levels exceeding 150 μmol m^{-2} s^{-1}) and photoperiod (more than 12 h of light per day), whereas the dissolved inorganic nitrogen decreased (to below 10 μM). Accordingly, considering the environmental requirements ([51, 66, 79, 91, 92], see details in Figure 5), the culture time frame of *U. pinnatifida* may be primarily related to lower temperatures (below 15−17°C) and nitrogen availability in seawater (above 5 μM); however, the harvesting time also could be related to the photoperiod (starting long-day (LD) photoperiod), as sporophyll formation (reproduction) is highly probable under the conditions associated with long days [93]. The annual sporophyte of *U. pinnatifida* should be harvested before they are fertile so that their growth stops and they initiate senescence (due to the reallocation of resources from blades to sporophylls) [64]. In contrast, the outplanting time for *S. latissima* mariculture coincided with decreases in temperature (below 15°C), irradiance (levels falling below 200 µmol m^{-2} s^{-1}) and photoperiod (less than 12 h of light per day), whereas dissolved inorganic nitrogen increased (to 5–10 µM). Harvesting time also coincided with increases in temperature (greater than 15°C), irradiance (levels exceeding 200 µmol m^{-2} s^{-1}) and photoperiod (more than 12 h of light per day), whereas dissolved inorganic nitrogen decreased (to below 1.4 µM) ([54, 94-99], see Figure 6). Based on these findings, the results obtained from our cultivation trials and the relevant environmental requirements (see details in Figure 6), the culture time frame of *S. latissima* might be primarily related to lower temperatures (below 15°C) and nitrogen availability in seawater (above 1.4 µM).

Seawater temperature and seawater nitrogen concentration are the key factors determining the optimal time frames (outplanting and harvesting periods) for the mariculture of *U. pinnatifida* and *S. latissima* along the Atlantic coast of southern Europe (northern Spain). This conclusion is in agreement with other studies performed in Asiatic waters, where similar relationships have been suggested for the mariculture of *U. pinnatifida* and *S. japonica* [66, 78-80, 89, 92, 100-102]. However, photoperiod is also a key factor defining the harvesting time of the annual species *U. pinnatifida*. In conclusion, an important aspect of the successful mariculture of *U. pinnatifida* and *S. latissima* in northern Spain, as in other potential farming regions, is that the culture time frames (outplanting and harvesting periods) should match the known requirements and conditions for the optimal growth of kelp. When well-defined cultivation periods are achieved in a particular region, much higher yields are obtained, as shown by the various cultivation trials performed during this study.

5. Methods for cultivation

The traditional methods of kelp cultivation developed for *U. pinnatifida* and *S. japonica* in Asian waters have been discussed in this review as a basis for the development and implementation of suitable methodologies for the mariculture of *U. pinnatifida* and *S. latissima* along the Atlantic coast of southern Europe (northern Spain). For the annual kelp *U. pinnatifida,* the same culturing method as a 1-year production cycle used for the commercial farming of this species in Asian waters has been adopted (see Figure 3). Nevertheless, the results of the present study indicate that the culture period at sea must be only 5–6 months because the favourable growing season for this species on the southern European Atlantic coast (northern Spain) (see Figures 2A and 5) is shorter than the well-defined sea culture period of 6–8 months in Asian waters [66, 68, 72]. Nevertheless, recent studies in Japan have shown that shortening the culture period to 4 months can be achieved by nitrate fertilization of the gametophytes and young sporophytes (about 2 cm in length) [101]. This method can be regarded as a “forced cultivation” to produce *U. pinnatifida* because the culture period at sea is reduced to advance the harvest date.

The most widely used cultivation methods for *S. japonica* in Asian countries, "forced cultivation" and cultivation by transplanting young fronds [36, 37, 78, 89], were successfully tested for the perennial kelp *S. latissima* in northern Spain [9, 28, 29]. To date, these methods have not been studied for this kelp in European waters. Initially, the cultivation method for Asian *Saccharina* was developed using a 2-year cycle of production because, in nature, sporophytes reach a harvestable size in approximately 20 months. However, Asiatic researchers have reduced *Saccharina* cultivation to 8 months using the "forced cultivation" method (see Figure 4 for more details). This method relies on early seedling production in the summer and results in lower costs for farmers [36, 37, 78, 89, 103]. The method for producing *S. latissima* in a 2-year cycle was initially tested on the Atlantic coast of Galicia (northern Spain), but it was not successful due to the high mortality of sporophytes throughout the summer season, which significantly reduced crop production [27]. Lee and Brinkhuis [88] reported similar observations for this kelp at its southern limit of distribution in northwestern Atlantic waters (Long Island Sound, New York). In addition, this 2-year cultivation cycle of *S. latissima* in Galicia was much more expensive than the "forced cultivation" method due to the necessary maintenance practices, resulting in increased production costs [27]. In contrast, the success of the "forced cultivation" method for *S. latissima* mariculture was demonstrated in subsequent studies. However, the "forced cultivation" of *S. latissima* required a shorter time period, 5−6 months, in the sea along the southern European Atlantic coast (Spain) because the favourable growing season for this species is also shorter within this southern area (summarized in Figures 2B and 6), as previously mentioned for *U. pinnatifida*. Finally, cultivation by transplanting young fronds is another method that uses sporophytes obtained from the thinning of plantings and involves the subsequent transplantation of excess individuals. This practice is common in Asian kelp farming and serves to improve the quality of the product for human consumption (see Figure 4) [36, 37, 104]. *S. latissima* cultivation using this transplanting method was determined to be feasible both technically and biologically, showing reasonably good growth and productivity in northern Spain [9]. This method could represent a potential alternative for later outplantings of this kelp species. Additionally, it could allow the grower to benefit from the thinning of fronds as both production and quality increase in "forced cultivation". The capacity of this species to develop new holdfasts from transplanted young sporophytes (allowing reattachment to culture ropes) indicates that this species can be used not only in commercial cultivation but also to restore areas where *S. latissima* has disappeared. Restoration by transplanting young fronds has already been used in some kelp species as a potential approach to environmental mitigation [105-107].

6. Introduced vs. native species in cultivation

6.1. Economic issues

Commercial-scale cultivation trials included in this review show that the mariculture of the native kelp *S. latissima* produced a higher yield than did the mariculture of the introduced kelp species, *U. pinnatifida*, along the Atlantic coast of southern Europe (northern Spain). Biomass yield is a factor of economic importance, and it can be used to compare the cost effectiveness of the two farmed kelps because the costs of setting up and operating a kelp farm are similar between the two species. In kelp farming, biomass is usually expressed per meter of culture rope because yield comparisons per unit farm area are more difficult. The reason for this difficulty is that different culture raft configurations can result in variable numbers and lengths of culture ropes and therefore different yields [108]. In addition, extrapolations of yield from small areas up to one hectare are likely to overestimate the productivity [109].

A standard yield obtained was 9.6 kg fresh m^{-1} rope for *U. pinnatifida* cultivation [19] and 16.1 kg fresh m^{-1} rope for *S. latissima* cultivation [29]. Both kelps were outplanted on hanging ropes in December at the moderately exposed site. These values for mean yields are similar to or markedly higher than those reported from other parts of the world for these kelp species. For *U. pinnatifida* cultivation, the results are comparable to the best yields obtained in previous experimental studies along the Atlantic coast of France and Spain (10 kg fresh m^{-1} rope) [17, 76] and to the yield range reported for commercial farms in their native Asian waters (5 to 10 kg fresh m^{-1} rope) [72]. The production values for *S. latissima* in northern Spain could even be improved up to 20 kg fresh m^{-1} rope by cultivation with earlier outplanting dates (November) at low culture depth (0−1 m), as has recently been obtained in Galicia [31]. Cultivation at the southern distribution limit of *S. latissima* allowed us to obtain higher yields compared with those reported in colder waters along the optimal distribution range of this species in the North Atlantic and Pacific oceans (4 to 9 kg fresh m^{-1} rope) [10, 70, 75].

This high productivity may occur at southern sites because *S. latissima* is extremely well adapted to broad latitudinal and depth gradients. Populations of this species are exposed to very different environmental conditions and show ecotypic differentiation (genetic accommodation or adaptation in intraspecific populations) between their northern and southern range limits in the North Atlantic Ocean with respect to light and temperature [110-115]. The Iberian Peninsula’s *S. latissima* sporophytes appear to perform well and be better adapted to the annual practice of early outplanting (i.e., “forced cultivation”) under the environmental conditions of its southern boundary distribution, as shown by the high yields obtained in this study. Additionally, the early sporophytes (seedlings) of the *S. latissima* used in our cultivation trials were produced from gametophyte stock cultures (germplasm collection) that originated from Iberian populations that have undergone successive inbreeding and directional selection. The possible influence of the Iberian ecotypes or selected cultivars on the yields obtained in our cultivation trials along the Atlantic coast of southern Europe (northern Spain) should be studied to determine the implications for cultivation practices in areas that may become warmer or more southern-like due to global climate change. Cultivars resistant to high temperature are used to extend or maintain *Saccharina* farming in warmer waters in Asia [116-119].

In addition, it is important that the chosen high-yield commercial kelp species have a high economic value because they can also be used in many value-added applications and services. Thus, it is necessary to have sufficient demand to support the development of commercial-scale mariculture to the extent that cultivation becomes economically feasible. Unlike *Undaria*, which is mainly used as human food, *Saccharina* and related kelps have been used for many other purposes. For example, they are used as raw material for the industrial extraction of valuable compounds such as alginate, in feed for aquaculture and animal husbandry, in agricultural fertilizers, as feedstock for biofuel production and for pharmaceutical, and cosmetic purposes [1, 2]. Therefore, there will be a well-established need for the production of *Saccharina* in the near future in Europe, and its uses and applications are expected to be integrated into *S. latissima* biorefineries and supplied by marine farming (summarized in Figure7). The kelp biorefinery concept can be defined as the sustainable processing of biomass into a spectrum of marketable products (e.g., food, chemicals, feed) and energy (e.g., bioethanol).

6.2. Environmental issues

In addition to its economic value, kelp mariculture can provide significant environmental benefits, such as carbon sequestration [120, 121] and bioremediation capacity to remove nutrients produced in coastal waters as a result of animal husbandry [122, 123] (summarized in Figure 7). In particular, *S. latissima* is considered one of the most suitable kelp species for incorporation into integrated multi-trophic aquaculture (IMTA), as it has already been successfully tested in Galicia (Spain) and other western countries [10-12, 31, 52, 124-127]. Additionally, kelp mariculture may help to not only increase production to meet commercial demands but also protect natural resources from overharvesting [128]. This benefit is of particular interest for *S. latissima* in northern Spain because this area is the southern limit of its distribution; here at the edge of its range, resources for its growth are very limited, and natural stocks have been threatened by the growing demand for human food. Kelp farming, as with kelp forests [3, 4], is expected to yield a significant environmental benefit by providing habitat and habitat resources for fauna and flora in coastal ecosystems.

Because both the introduced kelp *U. pinnatifida* and the native kelp *S. latissima* were cultivated during these trials, a discussion of their mariculture suitability from an ecological viewpoint is merited. The Asian kelp *U. pinnatifida* was deliberately introduced to the French Atlantic coast (Brittany) in 1983 for commercial farming by the French Institute for the Exploitation of the Sea (IFREMER) [17, 129-131]. The risk of escape from the farm sites and its establishment on the European Atlantic coast was considered minimal by the French authorities, but *U.*

pinnatifida was able to escape and form wild populations close to the farms [130, 131]. After a formal evaluation of its potential competition with native seaweed communities was conducted through an experimental control programme applied by Floc'h et al. [129], the potential impact of the industry was considered to be small, and the ICES Working Group on Introductions and Transfers of Marine Organisms allowed the farming of this species [132, 133]. However, since that time, the status of the introduced *U. pinnatifida* has changed greatly. Based on its dispersal potential and its ability to become established over a wide range, it is now considered one of the three most invasive seaweed species on the European Atlantic coast [134, 135]. In addition, it has also been listed in the book "100 of the World's Worst Invasive Alien Species", compiled by the International Union for Conservation of Nature (IUCN) [136]. However, studies focusing on its potential impact have found that establishment of this species has not deleteriously affected native flora or fauna either on the European Atlantic coast [129, 137] or in other places where it has been introduced [69, 138-142]. To date, only two reports of the biotic impacts of this species exist, for the lagoon of Venice, Italy [143] and Nuevo Gulf, Argentina [144]. Along the Galician coast, two decades after its introduction, all of the available evidence indicates that this Asian kelp has no appreciable impact because it occupies "empty" niches or disturbed communities [83]. Recently, the Spanish Government has enacted invasive alien species legislation to regulate the use (e.g., prohibiting cultivation) of well-known invaders that are already in the territory, but *U. pinnatifida* was not included as an invasive or potentially invasive species [145]. However, this kelp is considered to have the potential to modify rocky subtidal and intertidal communities due to its large size and ability to form dense stands, altering environmental conditions [67, 135, 140]. Currently, there is much controversy over whether its cultivation should be allowed in Europe. For example, French authorities now limit the farming of *U. pinnatifida* in those areas where it has been cultivated for a long time or where it forms dense stands, and farming is always under strict control to prevent potential ecological impacts and further spread [146].

In summary, the cultivation of *S. latissima* on the northern Spanish coast is highly recommended from an environmental standpoint, and the mariculture of this native species should be strongly promoted. However, projects to cultivate *U. pinnatifida* should first formally evaluate the potential ecological impacts, and the cultivation of the species should be restricted to particular areas of Galicia where it forms dense stands, pursued under strictly controlled conditions and conducted with a biomonitoring programme to minimize any risk.

7. Conclusions

The key conclusions of this review regarding the development and implementation of *U. pinnatifida* and *S. latissima* mariculture, as well as the mariculture of other kelps on a commercial basis along the Atlantic coast of Europe, particularly in northern Spain, are the following:

(1) Water movement is a key factor controlling the production and quality of kelp mariculture. *Undaria pinnatifida* is best cultured at more exposed sites rather than at sheltered sites, whereas both sheltered and exposed sites are suitable for *S. latissima* cultivation.

(2) Hanging rope culture is best suited for kelp mariculture in sheltered areas, whereas horizontal rope culture is better suited for exposed locations. The fixed-pole anchor system for raft culture has been used successfully in exposed open-ocean sites as an alternative to the traditional system with concrete blocks.

(3) The best outplanting dates for the mariculture *of U. pinnatifida* and *S. latissima* on the Atlantic coast of southern Europe are from October to November and from November to December, respectively. Harvesting is conducted from March to April and from April to May for these two outplanting seasons, respectively. Seawater temperature and seawater nitrogen concentration are the main determinants of the start and end of culture in the sea for both species.

(4) The sea cultivation method resembling the "forced cultivation" method used in Asia for *S. japonica* (kombu) is the best technique for *S. latissima* mariculture along the Atlantic coast of southern Europe (northern Spain).

(5) It is highly recommended that the native *S. latissima* be cultivated, as it is more economically and environmentally advantageous than the introduced kelp *U. pinnatifida*.

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Figure captions

Figure 1 Floating raft culture with concrete block (A) and fixed-pole (B) anchor systems and different culture rope systems: hanging rope method, vertical type (C1); horizontal rope method, long-line (C2); and hanging rope method, garland type (C3).

Figure 2 Summary diagram of cultivation of *Undaria pinnatifida* (A) and *Saccharina latissima* (B) along the Atlantic coast of southern Europe (northern Spain). The timing of the major culture stages for the optimal viability of the mariculture of these species in this region is shown.

Figure 3 Diagram summarizing the time frames for the outplanting and harvesting periods for the cultivation of *Undaria pinnatifida* in Japan in relationship to seawater temperature.

Traditional cultivation practices: adapted from culture data of Saito [66], Ohno and Matsuoka [68], Akiyama and Kurogi [72].

Current cultivation practices: adapted from data from Japanese farmers provided by an anonymous reviewer.

Temperature data from Saito [66], Akiyama and Kurogi [72] and Kawashima [36].

Figure 4 Diagram summarizing the time frames for the outplanting and harvesting periods for the cultivation of *Saccharina japonica* in Japan in relationship to seawater temperature.

Adapted from culture data of Kawashima [36] and temperature data of Kawashima [36].

Figure 5 Mariculture of *Undaria pinnatifida* in relationship to seawater temperature, dissolved inorganic nitrogen, underwater irradiance and day length in the waters of northern Spain.

The red dashed lines represent the following: optimal growth temperature of cultured sporophytes (T opt: 5−17°C) [66, 79, 92], half-saturation constant for nitrate uptake (Ks: 10−20 μM) [51], neutral day length (ND: 12:12 in hours of light:dark), saturating irradiance (Ek: 80−150 μmol m^{-2} s^{-1}) [51, 91].

Figure 6 Mariculture of *Saccharina latissima* in relationship to seawater temperature, dissolved inorganic nitrogen, underwater irradiance and daylength in the waters of northern Spain.

The red dashed lines represent the following: optimal growth temperature of sporophytes (T opt: 10−15°C) [96, 98, 99], half-saturation constant for nitrate uptake (Ks: 1,4 μM); [54], neutral day length (ND: 12:12 in hours of light:dark), saturating irradiance (Ek: 150−200 μmol m^{-2} s^{-1}) [94, 95, 97].

Figure 7 Scheme of the farming of native kelp, *Saccharina latissima*, to produce valuable products through the integrated biorefinery approach. The establishment of a kelp farm in northern Spain would provide economic and environmental benefits.

Figure 1

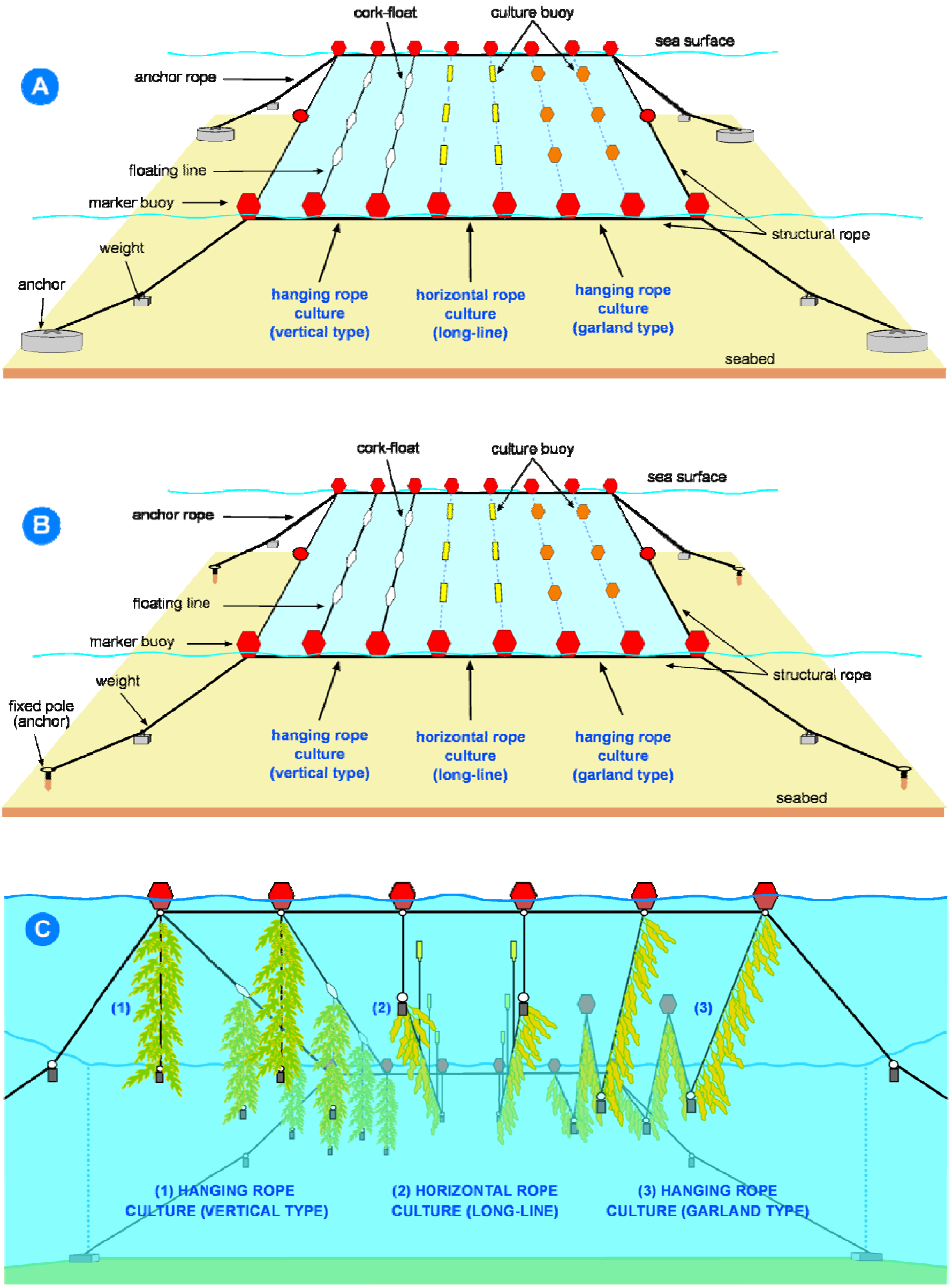

A
cork-float
culture buoy
sea surface
anchor rope
floating line
marker buoy
structural rope
weight
anchor
hanging rope culture (vertical type)
horizontal rope culture (long-line)
hanging rope culture (garland type)
seabed
B
cork-float
culture buoy
sea surface
anchor rope
floating line
marker buoy
structural rope
weight
fixed pole (anchor)
hanging rope culture (vertical type)
horizontal rope culture (long-line)
hanging rope culture (garland type)
seabed
C
(1)
(2)
(3)
(1) HANGING ROPE CULTURE (VERTICAL TYPE)
(2) HORIZONTAL ROPE CULTURE (LONG-LINE)
(3) HANGING ROPE CULTURE (GARLAND TYPE)

Figure 2a

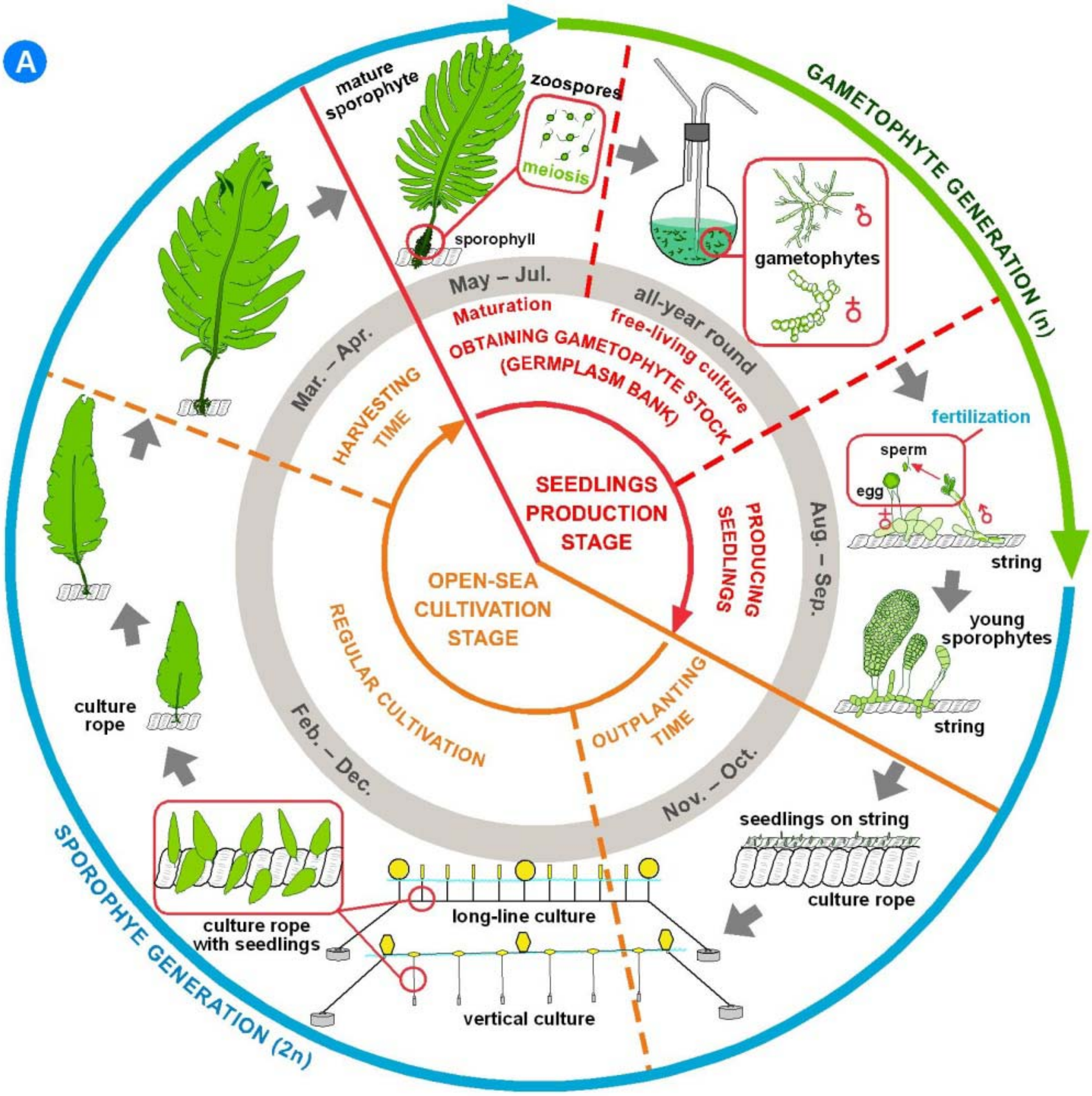

A
mature sporophyte
zoospores
meiosis
sporophyll
GAMETOPHYTE GENERATION (n)
gametophytes
♂
♀
fertilization
sperm
egg
♀
♂
string
young sporophytes
string
seedlings on string
culture rope
long-line culture
culture rope with seedlings
vertical culture
SPOROPHYTE GENERATION (2n)
culture rope
May – Jul.
all-year round
Aug. – Sep.
Nov. – Oct.
Feb. – Dec.
Mar. – Apr.
Maturation
free-living culture
OBTAINING GAMETOPHYTE STOCK
(GERMPLASM BANK)
SEEDLINGS PRODUCTION STAGE
PRODUCING SEEDLINGS
OUTPLANTING TIME
OPEN-SEA CULTIVATION STAGE
REGULAR CULTIVATION
HARVESTING TIME

Figure 2b

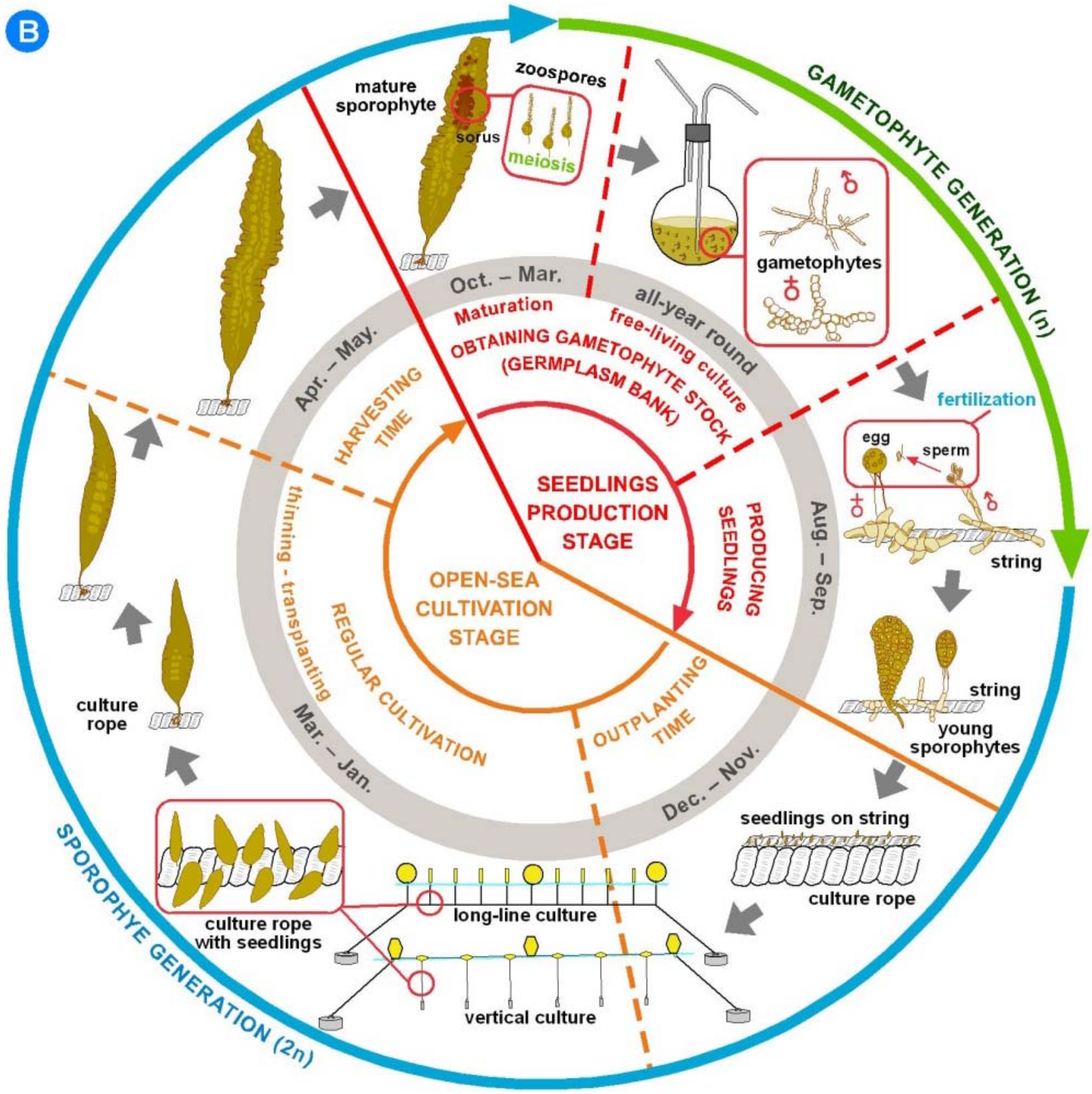

B
GAMETOPHYTE GENERATION (n)
SPOROPHYTE GENERATION (2n)
mature sporophyte
sorus
zoospores
meiosis
gametophytes
♂
♀
fertilization
egg
sperm
♀
♂
string
string
young sporophytes
seedlings on string
culture rope
long-line culture
vertical culture
culture rope with seedlings
culture rope
Oct. – Mar.
all-year round
Aug. – Sep.
Dec. – Nov.
Mar. – Jan.
Apr. – May.
Maturation
OBTAINING GAMETOPHYTE STOCK (GERMPLASM BANK)
free-living culture
SEEDLINGS PRODUCTION STAGE
PRODUCING SEEDLINGS
OUTPLANTING TIME
REGULAR CULTIVATION
thinning - transplanting
HARVESTING TIME
OPEN-SEA CULTIVATION STAGE

Figure 3

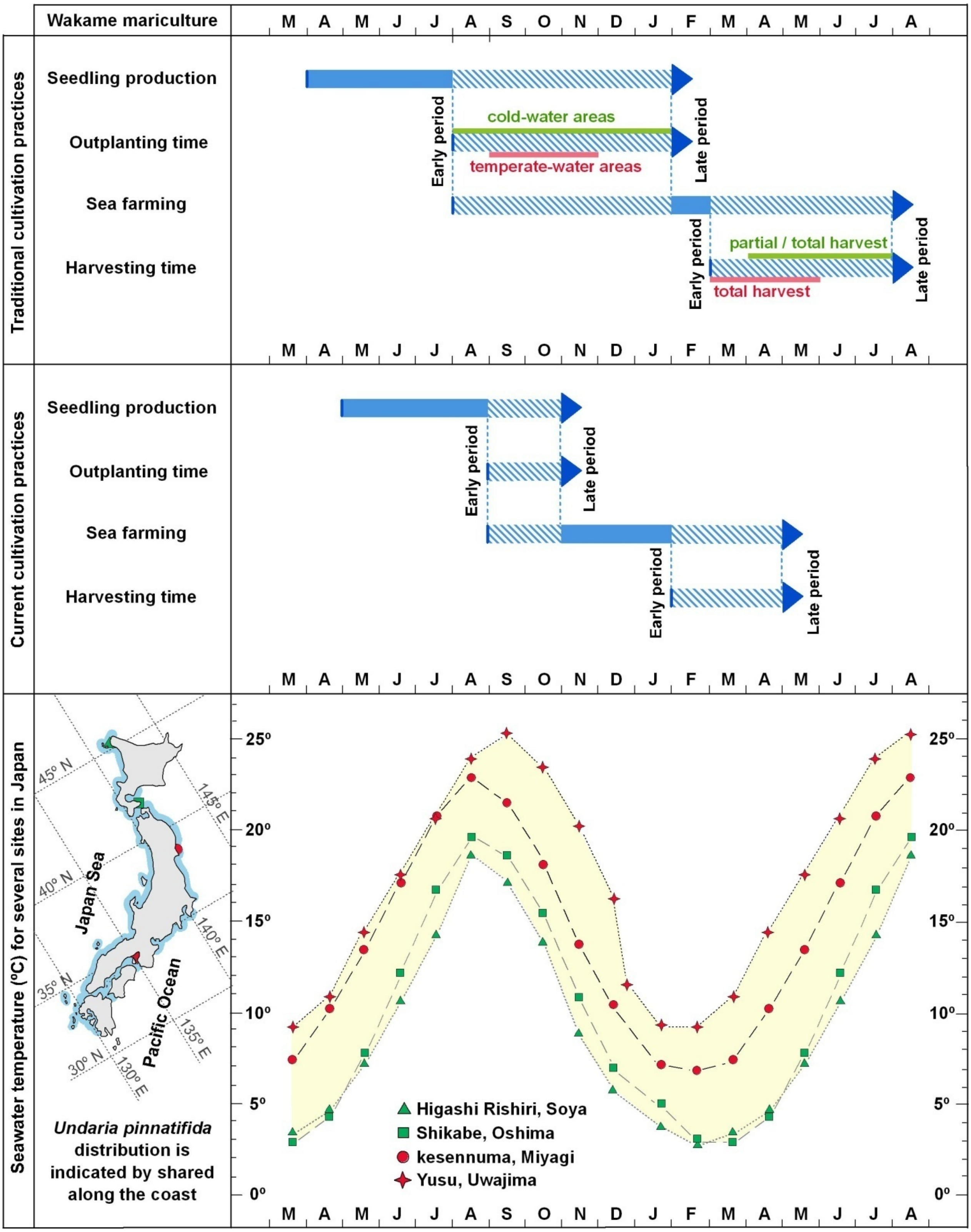

Wakame mariculture
M A M J J A S O N D J F M A M J J A
Traditional cultivation practices
Seedling production
Outplanting time
Sea farming
Harvesting time
Early period
Late period
cold-water areas
temperate-water areas
partial / total harvest
total harvest
Current cultivation practices
Seedling production
Outplanting time
Sea farming
Harvesting time
Early period
Late period
Seawater temperature (ºC) for several sites in Japan
45º N
40º N
35º N
30º N
145º E
140º E
135º E
130º E
Japan Sea
Pacific Ocean
Undaria pinnatifida distribution is indicated by shared along the coast
25º
20º
15º
10º
5º
0º
Higashi Rishiri, Soya
Shikabe, Oshima
kesennuma, Miyagi
Yusu, Uwajima

Figure 4

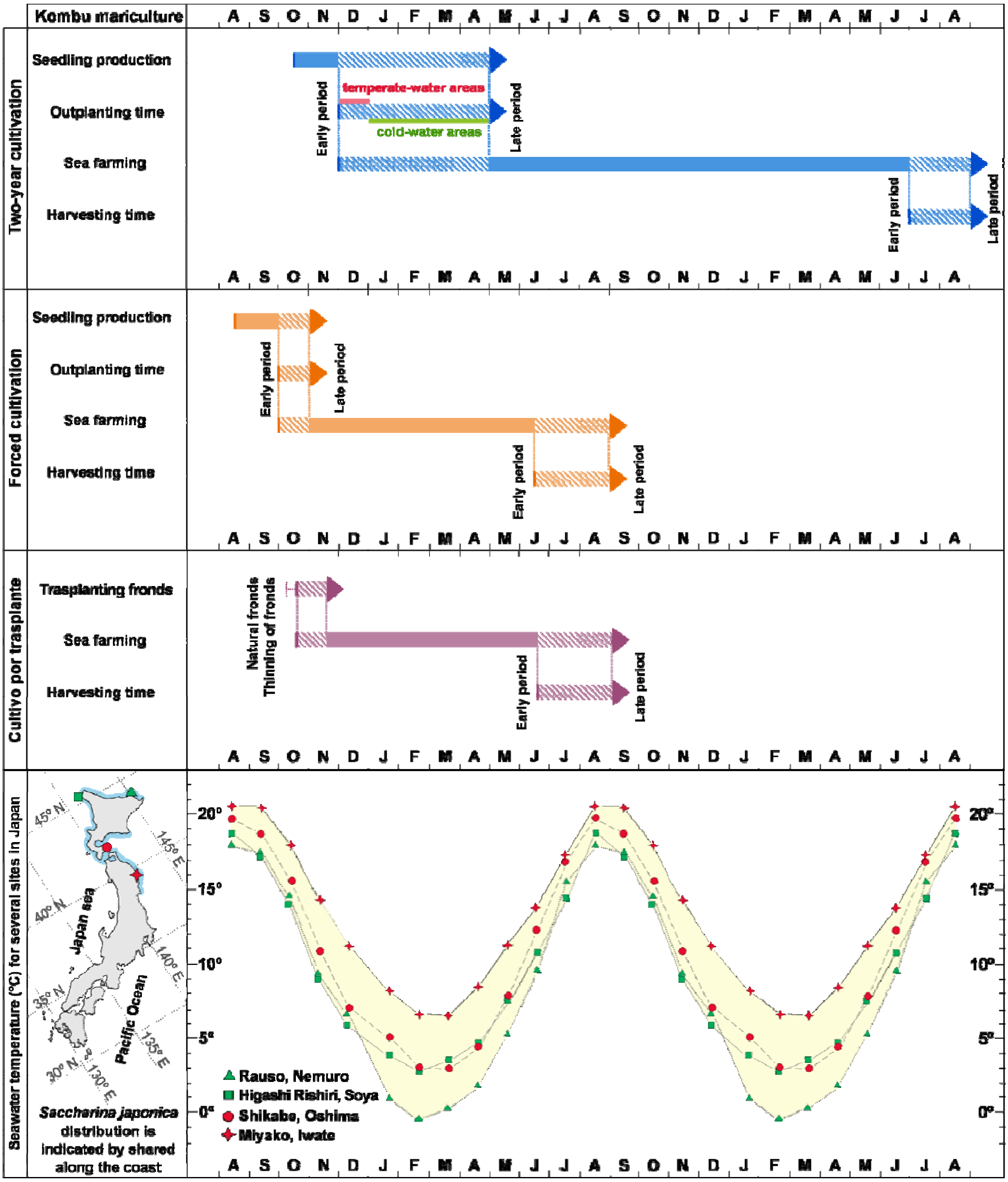
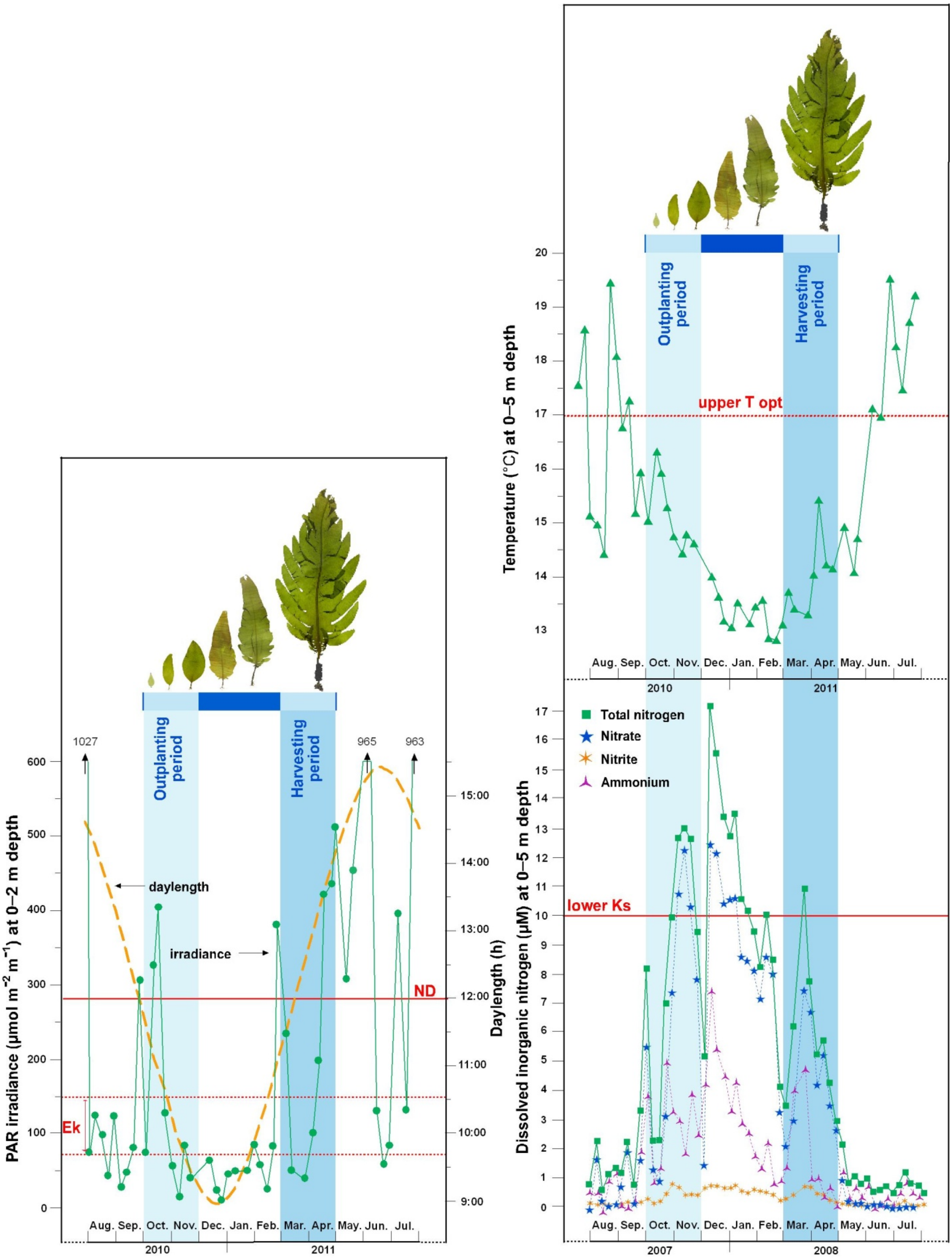
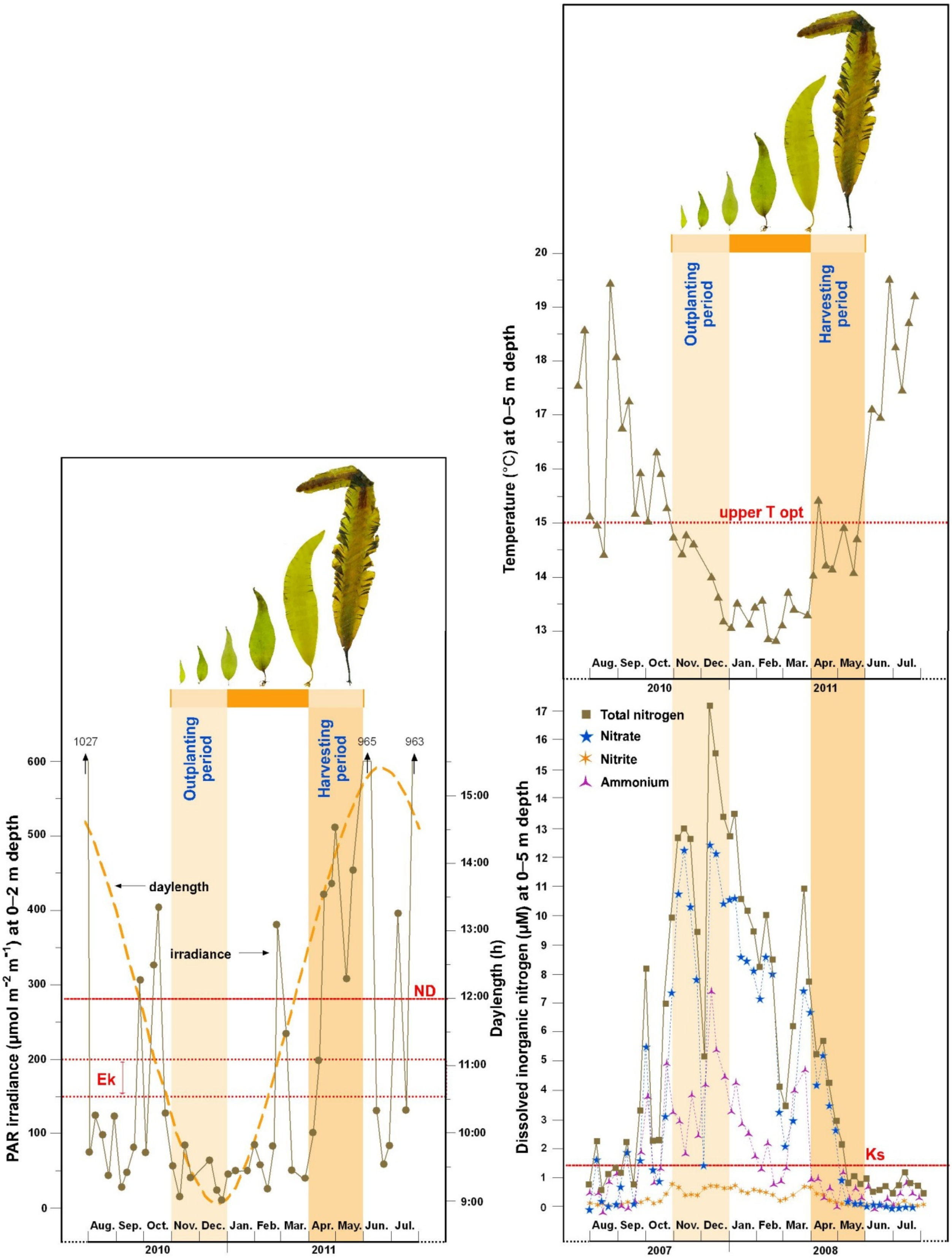

Kombu mariculture
A S O N D J F M A M J J A S O N D J F M A M J J A
Two-year cultivation
Seedling production
Outplanting time
Sea farming
Harvesting time
Early period
Late period
temperate-water areas
cold-water areas
Forced cultivation
Cultivo por trasplante
Trasplanting fronds
Natural fronds
Thinning of fronds
Seawater temperature (°C) for several sites in Japan
45° N
40° N
35° N
30° N
145° E
140° E
135° E
130° E
Japan sea
Pacific Ocean
Saccharina japonica distribution is indicated by shared along the coast
20°
15°
10°
5°
0°
▲ Rauso, Nemuro
■ Higashi Rishiri, Soya
● Shikabe, Oshima
✦ Miyako, Iwate

Figure 5



PAR irradiance (μmol m⁻² m⁻¹) at 0–2 m depth
Daylength (h)
1027
965
963
600
500
400
300
200
100
0
15:00
14:00
13:00
12:00
11:00
10:00
9:00
Outplanting period
Harvesting period
daylength
irradiance
ND
Ek
Aug. Sep. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May. Jun. Jul.
2010
2011
Temperature (°C) at 0–5 m depth
20
19
18
17
16
15
14
13
upper T opt
Dissolved inorganic nitrogen (μM) at 0–5 m depth
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
Total nitrogen
Nitrate
Nitrite
Ammonium
lower Ks
2007
2008

Figure 6



1027
965
963
600
500
400
300
200
100
0
PAR irradiance (µmol m^{-2} m^{-1}) at 0–2 m depth
daylength
irradiance
ND
Ek
Outplanting period
Harvesting period
15:00
14:00
13:00
12:00
11:00
10:00
9:00
Daylength (h)
Aug. Sep. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May. Jun. Jul.
2010
2011
20
19
18
17
16
15
14
13
Temperature (°C) at 0–5 m depth
upper T opt
Aug. Sep. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May. Jun. Jul.
2010
2011
17
16
15
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13
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11
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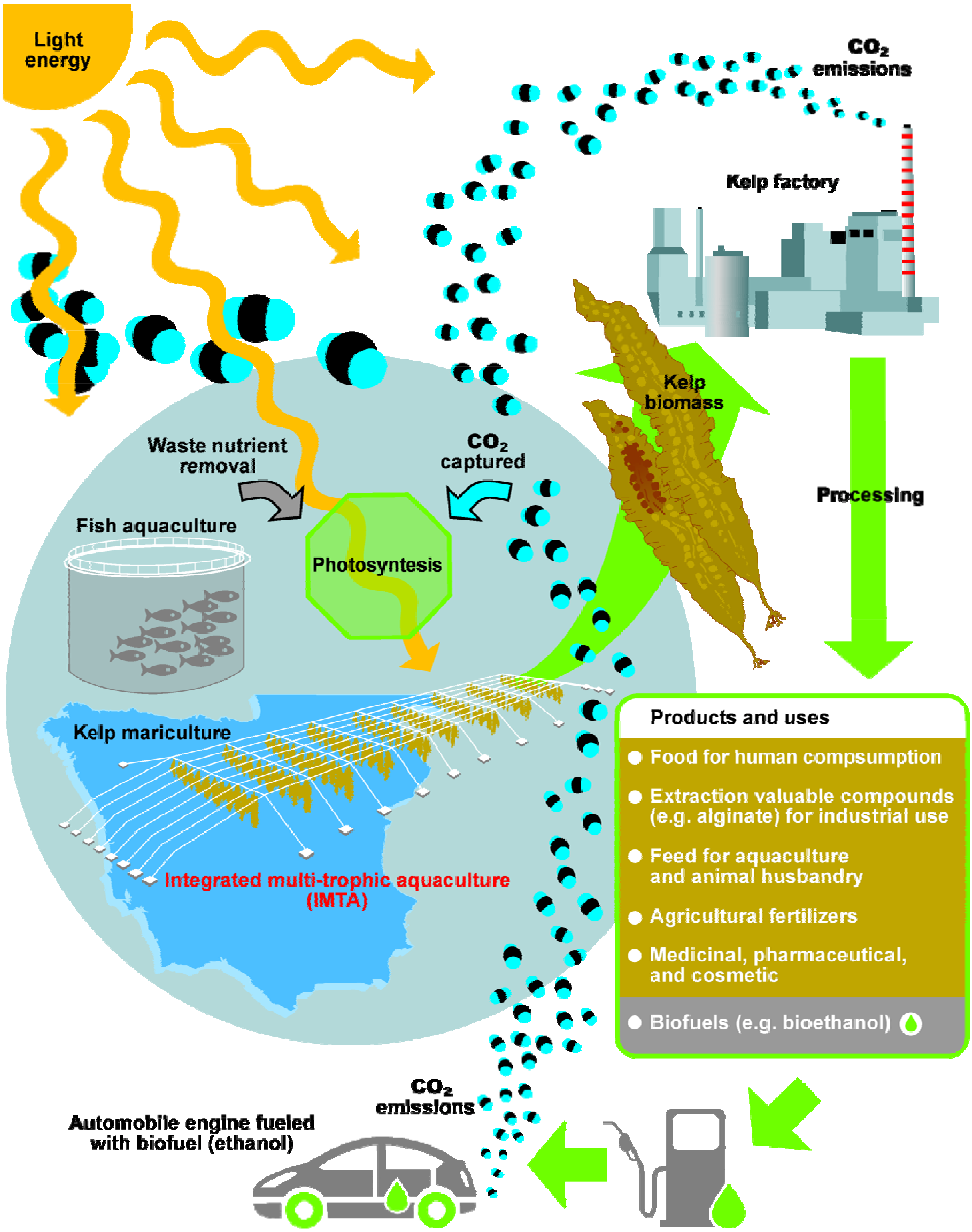
7
6
5
4
3
2
1
0
Total nitrogen
Nitrate
Nitrite
Ammonium
Dissolved inorganic nitrogen (µM) at 0–5 m depth
Ks
Aug. Sep. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May. Jun. Jul.
2007
2008

Figure 7


Light energy
CO₂ emissions
Kelp factory
Kelp biomass
Processing
Waste nutrient removal
CO₂ captured
Fish aquaculture
Photosyntesis
Kelp mariculture
Integrated multi-trophic aquaculture (IMTA)
Products and uses
Food for human compsumption
Extraction valuable compounds (e.g. alginate) for industrial use
Feed for aquaculture and animal husbandry
Agricultural fertilizers
Medicinal, pharmaceutical, and cosmetic
Biofuels (e.g. bioethanol)
CO₂ emissions
Automobile engine fueled with biofuel (ethanol)