Seaweed future cultivation in Chile: perspectives and challenges

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Abstract: Production of seaweeds in Chile has fluctuated between 120,000 and 316,000 wet metric tons per year during the last ten years. The most important Phaeophyta are exploited for alginate production and as abalone feed. Among the Rhodophyta, Chilean production comes mainly from wild stocks, as at present cultivation on a commercial scale is restricted to *Gracilaria*. Large-scale production of this species has been the result of a sharp increase in the number of farms. During the last five years an important trend towards diversification of seaweed exploitation and cultivation has developed. The demand for brown algal materials for the alginate industry, abalone cultivation, seaweed flour production for human and animal feeding and the development of novel food products has encouraged the farming of *Macrocystis pyrifera* and of red edible seaweeds, such as *Chondracanthus chamissoi* and *Callophyllis variegata*, is also promoting the development of cultivation activities.

Keywords: Chile; Phaeophyta; research developments; Rhodophyta; seaweed cultivation.

Reference to this paper should be made as follows: Buschmann, A.H., Hernández-González, M.C. and Varela, D. (2008) 'Seaweed future cultivation in Chile: perspectives and challenges', *Int. J. Environment and Pollution*, Vol. 33, No. 4, pp.432–456.

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1 Introduction

Over the last 15 years, seaweed research and use in Chile has entered a phase characterised by the development of

- an industrial capacity to produce and process algae
- a scientific capacity to study seaweeds
- a closer but still weak relationship between scientists and industry (Santelices, 1996).

In this scenario, seaweed harvesting in Chile reached a maximum 322,000 wet metric tons per annum in 1996, involving various species of Phaeophyta and Rhodophyta. The most important Phaeophyta are *Lessonia nigrescens, L. trabeculata*, *Macrocystis pyrifera, M. integrifolia* and *Durvillaea antarctica* (Figure 1). These seaweeds are exploited for alginate production and recently also as abalone feed. Among the Rhodophyta, the most important harvested species are the carrageenophytes *Sarcothalia crispata*, *Mazzaella laminarioides*, *Gigartina skottsbergii*, *Chondrocanthus chamissoi* (Figure 2) and the agarophytes *Gracilaria chilensis* (Figure 2(a)) and *Gelidium lingulatum* (Norambuena, 1996). Other taxa, which also contribute to the harvested biomass, although to a lesser extent, are *Gelidium rex*, *Mazzaella membranacea*, *Ahnfeltia plicata*, *Ahnfeltiopsis furcellata*, *Porphyra columbina* (Figure 2(c)), *Callophyllis variegata* (Figure 2(d)), *Mastocarpus papillatus* and *Chondrus canaliculatus* (Norambuena, 1996). Algal production in Chile is mainly based on the exploitation of wild stocks whereas cultivation on a commercial scale remains restricted to *Gracilaria chilensis* (Santelices and Ugarte, 1987; Buschmann et al., 1995, 2001a; Norambuena, 1996), but diversification of this aquaculture industry is developing very fast.

The main objective of this contribution is to summarise the present state of knowledge of brown and red seaweed exploitation and cultivation in Chile. We address this issue by reviewing both land catch statistics exports and advances in recent biological knowledge. These advances include propagation methods, culture conditions and techniques, product quality assessment, pest management and strain selection, factors which are foreseen as the basis for diversifying brown and red seaweed farming in Chile.

Figure 1 Economically important Phaeophyta from Chile: (A) *Lessonia nigrescens*; (B) *Durvillaea antarctica* and (C) *Macrocystis pyrifera*

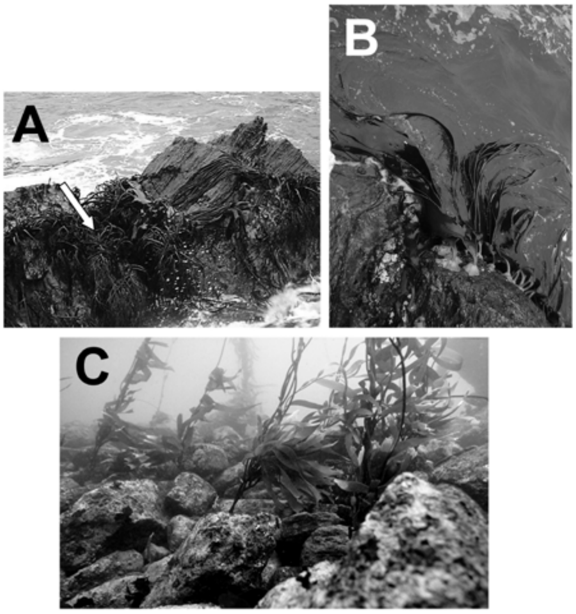
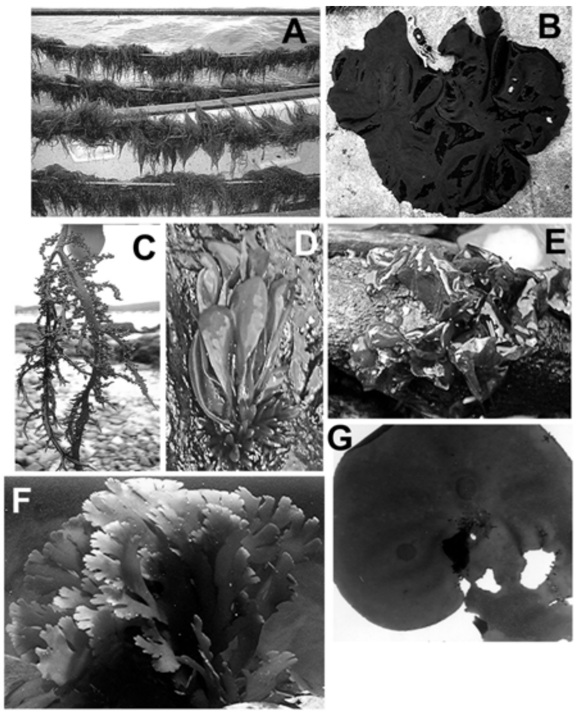


Figure 2 Economically important Rhodophyta from Chile: (a) *Gracilaria chilensis*; (b) *Sarcothalia crispata*; (c) *Chondracanthus chamissoi*; (d) *Mazzaella laminarioides*; (e) *Porphyra columbina*; (f) *Callophyllis variegata* and (g) *Gigartina skottsbergii*



2 Seaweed exploitation in Chile

The total landings of brown algae and red seaweeds reached over 300,000 metric tons during the last few years (Figure 3). It is important to mention that during the past two years a strong decline in the landings of brown algae has occurred. It has been suggested that this is due to over harvesting by abalone farmers in northern Chile. The brown alga that shows the greatest demand is *Lessonia*, with landings of 96,428 metric tons in 2002 (Figure 4), mainly carried in northern Chile. On the other hand, the interest for *Macrocystis* is increasing due to the demand caused by abalone farmers (Vásquez and Vega, 1999) and the development of new products such as organic fertilisers and use for human food; however, landings still do not show this trend (Figure 4). *Durvillaea antarctica* has been used as a food source for centuries in Chile, with landings that are inferior to 2,500 metric tons (Figure 4). These data must be analysed with caution as the data collection in remote areas could be subject to some errors.

Figure 3 Total landings (wet tons) of brown (●) and red (◆) seaweeds in Chile

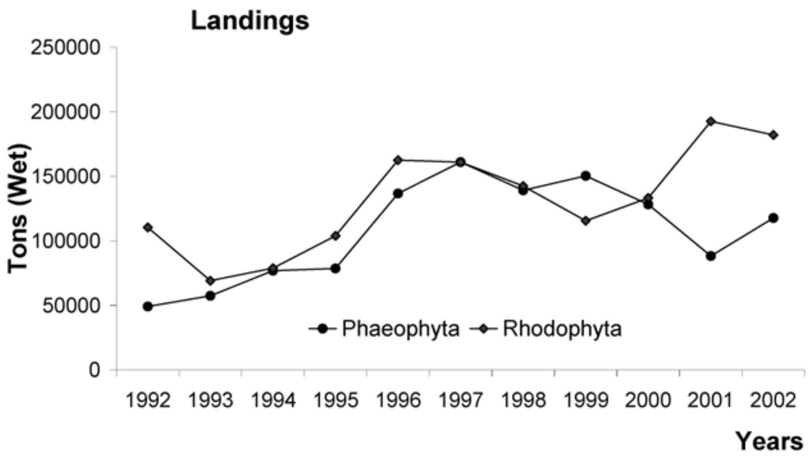
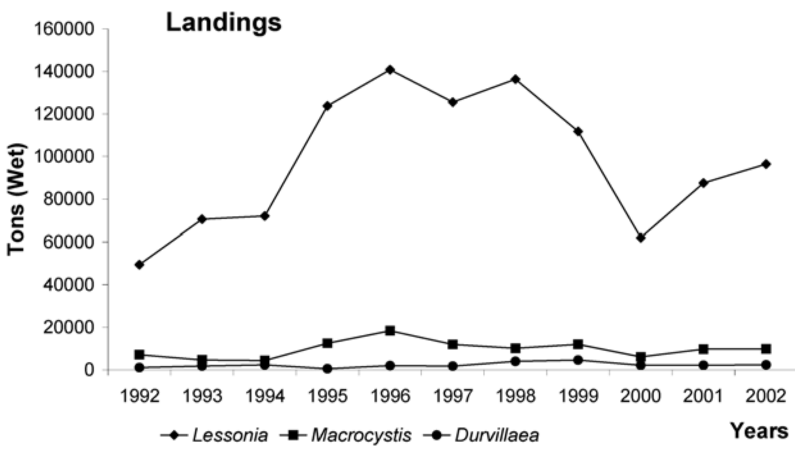


Figure 4 Landings (wet tons) of brown seaweeds: *Lessonia* spp. (◆); *Macrocystis* spp. (■) and *Durvillaea antarctica* (●) in Chile



Red algal species are predominantly harvested in southern Chile for direct use as food or as raw material for agar and carrageenan extraction. The most commonly exploited agarophytes are *Gracilaria chilensis*, *Ahnfeltia plicata*, and *Gelidium lingulatum*. Exploitation of natural *G. chilensis* beds reached a peak in 1985 and was followed by a gradual but steady decline during the following years due to over-harvesting, and unfavourable market conditions (Norambuena, 1996). However, during 1995 and 1996, with over 120,000 wet tons, production level was again as high as 1985 (Figure 5) as a result of management strategies and the establishment of over 500 new farming operations (Buschmann et al., 2001a). At present the cultivated production of *Gracilaria* has decreased to only a few tons per year (Figure 5) as a result of unfavourable market conditions (Figure 6). On the other hand, exploitation of *G. lingulatum* fluctuated between 800 and 1,600 wet tons during the last ten years, whereas *Ahnfeltia* has been exploited erratically and only in small amounts (Buschmann et al., 2001a).

Figure 5 Landings (wet tons) of *Gracilaria chilensis*: cultivated (■) and total *Gracilaria* (●) in Chile

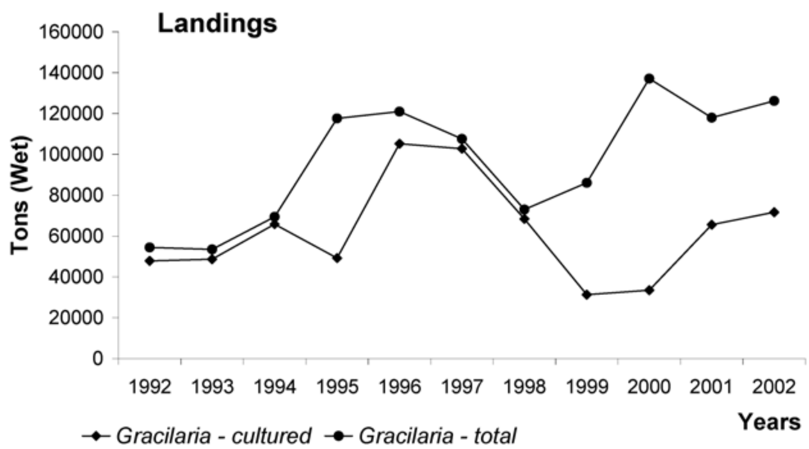
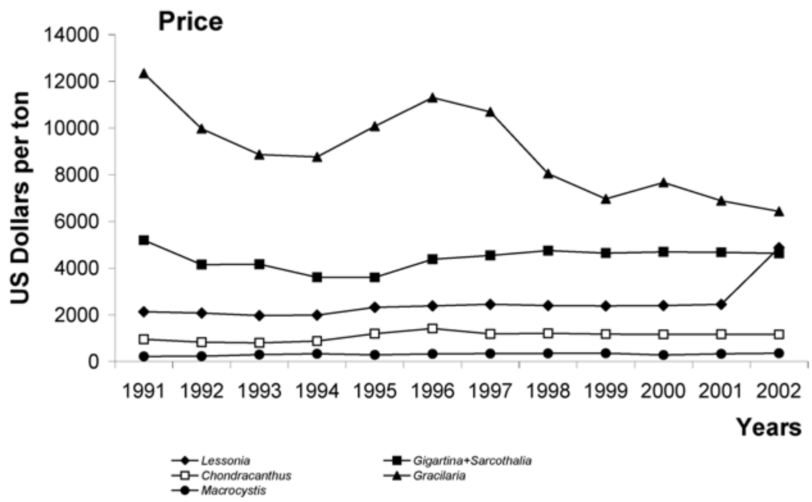
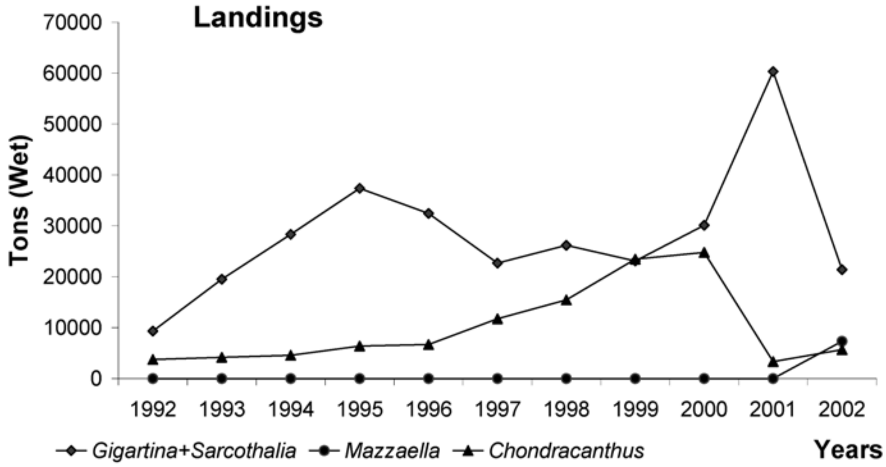


Figure 6 Prizes (US$ per ton) of red and brown seaweeds in Chile



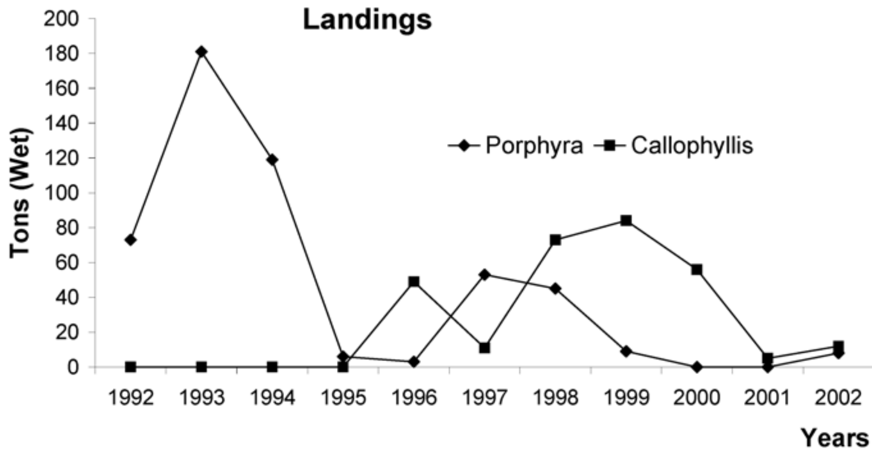
The carrageenophytic algal genera mostly exploited in Chile include *Gigartina*, *Sarcothalia, Chondracanthus*, and *Mazzaella* (Figure 7). The landings and price of these species has not increased substantially during the last ten years (Figure 6). Significantly lower biomass has been obtained from *Gymnogongrus furcellatus* stands (Buschmann et al., 1999a).

Figure 7 Landings (tons) of carrageenophytes in Chile: (a) *Gigartina* + *Sarcothalia* (◆); (b) *Mazzaella laminarioides* (●) and (c) *Chondranthus chamissoi* (π)



Edible seaweeds have also been traditionally exploited in Chile. Landings of the red alga *Porphyra columbina* vary from a few tons to more than 180 wet tons per year (Figure 8). Another exploited Rhodophyta is *Callophyllis variegata* (Figure 8), which has a promising future due to its high commercial value, currently at almost 30 US$ per dry kg. As indicated above, *Chondracanthus chamissoi* is another species presently exploited and processed as dry algae (Vásquez and Vega, 2001).

Figure 8 Landings (tons) of edible red algae in Chile: (a) *Porphyra columbina* (◆) and (b) *Callophyllis variegata* (■)



Seaweed processing in Chile has increased substantially in recent years. During the last eight years, the export of dry seaweeds has been stable with returns of approximately US$ 22 million per annum (Figure 9). Agar production and export reached a total of 2290.2 tons in 1997, experiencing a decline by 1998 and recovering afterwards to 2400.6 tons in 2002 (Figure 10). On the other hand, carrageenan production, which began in 1990, has increased steadily to a current production of 3443.6 tons in 2002 (Figure 10). Exports of these polysaccharides generated returns of more than US$25 million, plus US$35 million of agar in 2002 (Figure 9). Thus, in 1996 the Chilean seaweed industry as a whole, contributed with revenues of ca. US$90 million, with agar exports as the most important item (Figure 9). Due to the oriental economic crisis of 1998–1999, returns to Chile have declined. However, the seaweed incomes increased again to US$84 million in 2002 (Figure 9).

Figure 9 Exportations (US$ × 1000) of different seaweed products: dry algae (■); agar (π); carrageenan (■); alginate (●) and colagar (♬)

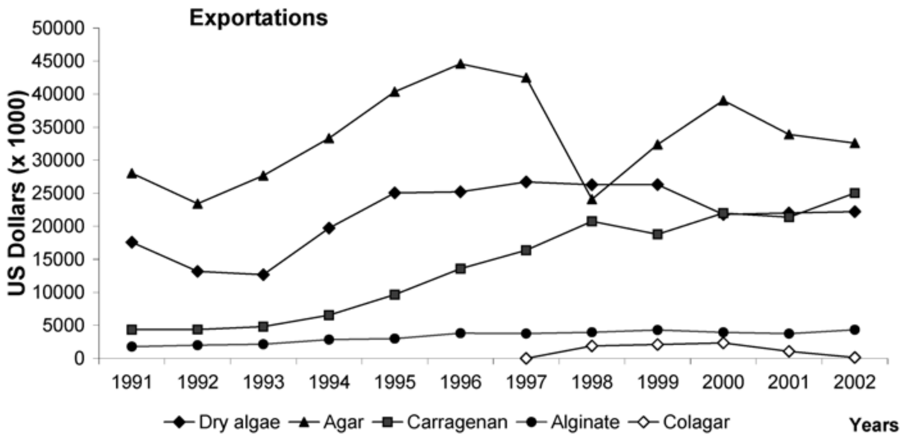
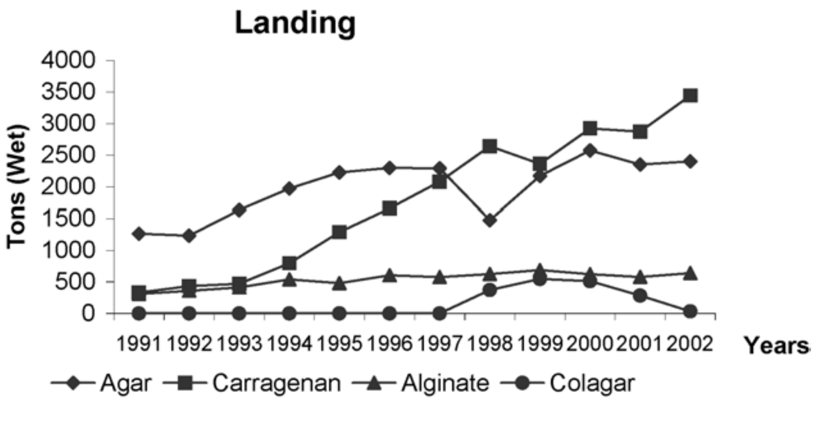


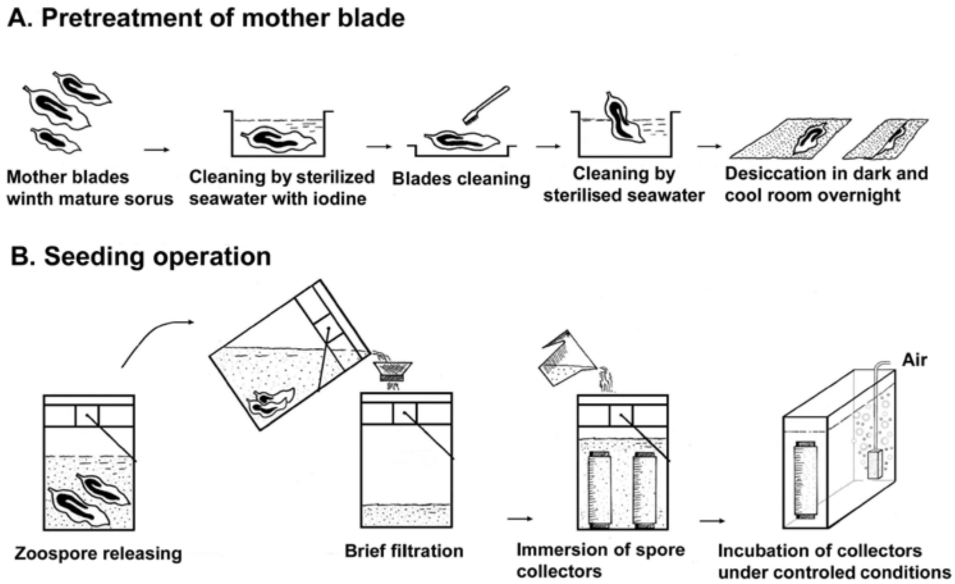
Figure 10 Landings (wet tons) of seaweed for obtaining different products: agar (■); carrageenan (■); alginate (π) and colagar (★)



3 Phaeophyta cultivation

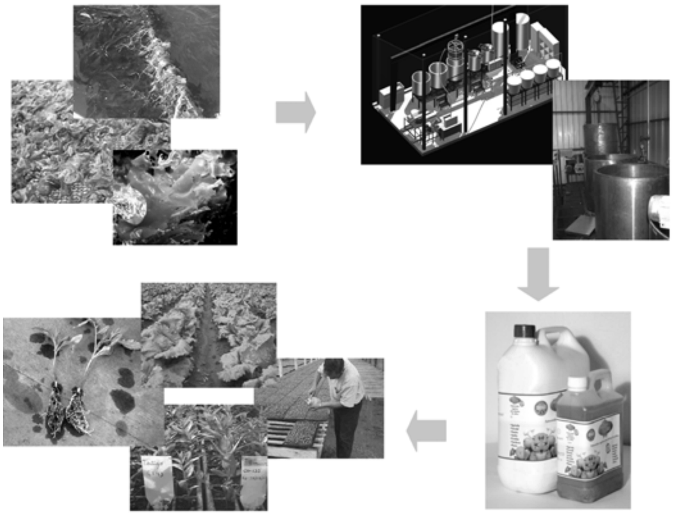
Species like *Laminaria japonica* and *Undaria pinnatifida* are massively cultivated for human consumption in oriental countries, but in Chile cultivation of brown algae is just starting. *Lessonia trabeculata*, *L. nigrescens* and *Macrocystis pyrifera* are collected for alginate. *M. pyrifera* and *L. nigrescens* have been harvested over the last few years for abalone feeding, whereas the bull kelp *Durvillaea antarctica* is used locally for human consumption. Experimental cultivation of *Lessonia* has been carried out in northern Chile (Edding et al., 1990; Tala et al., 2004) whereas culture conditions for *L. nigrescens* have been resolved (Avila et al., 1985). Hatchery (Figure 11) and pilot cultures for *Macrocystis* have also been successful in southern Chile (Gutiérrez et al., 2006). As a result of the expanding abalone industry in Chile there is also great interest in the culture of *M. pyrifera* in open sea (Vásquez and Vega, 1999). Furthermore, pilot scale cultures of this kelp are currently being carried out in southern Chile for the production of organic fertilisers and novel food products (Figure 12). Additionally, *M. pyrifera* appears to be a good candidate for bioremediation use for controlling salmon farm N-release in southern Chile (see Buschmann et al., 2001c; Chopin et al., 2001). However, optimisation of culture techniques must be adjusted to Chilean environmental conditions and some unique population features (Buschmann et al., 2004b, 2006) that require additional studies in order to ensure high quality products.

Figure 11 Phases for sporulation and rope seeding in *Macrocystis pyrifera*



Source: Modified from Merrill and Gillingham (1991)

Figure 12 Phases for obtaining organic fertilisers from *Macrocystis pyrifera* and *Ulva rigida* and tests using different plant crops that had a very significant improvement after the application of Macromix™



4 Rhodophyta cultivation

It has been indicated that in spite of *Gracilaria chilensis* morphological variation, Chilean *Gracilaria* correspond to only one species (González et al., 1996; Meneses, 1996; Candia et al., 1999), although the existence of a sibling species has been very recently reported (Cohen et al., 2004). Cost-benefit analyses indicate that in Chile *Gracilaria chilensis* farming (Figure 13) is economically profitable (Pizarro, 1986; Martínez et al., 1990; Buschmann et al., 1995), which has recently stimulated. The agar from *G. chilensis* has a greater resistance to hydrolysis during storage and a high ‘sugar reactivity’ (Arminsen, 1995), characteristics which determine the high demand for Chilean *Gracilaria* from the food industry. Because prices have been highly variable over the past ten years (Buschmann et al., 1995), it is important to optimise production by lowering costs and increasing productivity through the establishment of better management strategies. Farming of *G. chilensis* was possible because of the existence of a basic understanding of key biological aspects, such as propagation methods and ecophysiological responses under cultivation conditions, which allowed the development of large-scale planting methodologies (Pizarro, 1986; Pizarro and Barrales, 1986; Santelices and Ugarte, 1987; Westermeier et al., 1988a; Buschmann et al., 1995). Planting techniques have to fasten *Gracilaria* to the substratum have been described in detail by Alveal (1986), Pizarro (1986) and Buschmann et al. (1995). All planting techniques rely upon the capacity of *Gracilaria* to develop an underground thallus system (Santelices and Fonck, 1979; Santelices et al., 1984) which anchors the algae to the soft bottom. After planting, beds are maintained by vegetative growth from the underground thallus system, which is able to survive burial for several months. Artificially planted areas show the same seasonal pattern of wild stock biomass fluctuation (Pizarro, 1986; Santelices and Doty, 1989). This seasonal pattern is characterised by high growth rates during spring, followed by a decline toward summer and lowest growth in winter. Storms that naturally remove biomass and human harvesting are the main factors modifying the seasonal pattern of biomass growth in *Gracilaria* (Pizarro, 1986).

Figure 13 Photograph showing a subtidal *Gracilaria chilensis* farm in southern Chile

For subtidal areas in southern Chile, it has been established that *Gracilaria* production can reach 91–149 tons ha^{-1} yr^{-1} (Westermeier et al., 1991). In contrast, intertidal systems from similar latitudes are less productive, with biomass levels never exceeding 72 tons ha^{-1} yr^{-1} (Buschmann et al., 1995). On the other hand, in northern Chile production can be even higher (Pizarro, 1986), a phenomenon apparently related to higher temperatures and longer light regimes; oceanographic conditions that also have a major influence on production (Pizarro and Santelices, 1993). Harvesting frequency, planting biomass (see review in Buschmann et al. (1995)), and spatial arrangement of the inoculum (Santelices et al., 1993) are other important factors that determine the production capacity of a farming area. Different tools for harvesting *Gracilaria* in subtidal systems have been tested, either from boats or by divers (Santelices et al., 1984; Westermeier et al., 1988b). Suspended altures have been also tested producing good production responses (Westermeier et al., 1993), but cost and high epiphytism has reduced the enthusiasm for this type of work.

One of the common problems detected in farms is an abrupt drop in productivity, which is always preceded by 2–3 years of high yields. It is believed that this situation is the result of thallus aging, and seems to be influenced by the harvesting method. *Gracilaria* has apical meristems which are continuously removed during each harvesting period, leaving only the older parts of the thalli behind. To overcome the problem of decreased productivity, some farmers have tried to renew the cultured stock by using ropes seeded with carpospores (Alveal et al., 1997). This initiative has been applied in southern Chile and many areas are now planted with plants originated from spores (R. Rojas, personal communication). As an alternative hypothesis it has been suggested that lower productivity is in many cases a consequence of repeated harvesting that cause the loss of stocking algae (Buschmann et al., 1995). Recent results with *G. ferox* indicate that the growth potential of a specific strain can be maintained over extensive periods of intensive cultivation (Capo et al., 1999). Similar results have been obtained in tank cultures using *G. chilensis* (Retamales et al., 1994), suggesting that aging is unlikely to occur (Halling, 2004). This means that the issue of agronomic diligence is highly relevant to maintain a stable production of a *Gracilaria* farm.

A further challenge in *Gracilaria* cultivation is strain selection. The over-exploitation of several wild *Gracilaria* stands could be a limiting factor for further development of farming activities, because some of the larger genetic reserves for the species have been destroyed (Vásquez and Westermeier, 1993). To obtain plants with desirable characteristics, *Gracilaria* has been propagated by green-house sporulation and subsequent seeding of nylon ropes (Alveal et al., 1997) with field-collected spores (Buschmann and Kuschel, 1988), or via tissue culture (Collantes et al., 1990). Research has also been undertaken on the screening of *Gracilaria* populations, in search of better responses to some environmental factors (Santelices and Ugarte, 1990). Unfortunately, available information indicates that various commercially desirable characteristics of *Gracilaria* do not respond in the same way to abiotic and biotic factors, and therefore selection of a specific trait may unintentionally select another that may be negative for productive purposes (Buschmann et al., 1992).

Several types of genetic changes can modify the phenotypic expression of selected strains. It has been reported that *G. tikvahiae* shows an important degree of intraspecific variation apparently related to mitotic recombinations (van der Meer and Todd, 1977) and transposable genetic elements (van der Meer and Zhang, 1988). These sources of variability explain the great variation in morphological and growth responses of *Gracilaria* in the field and in the laboratory (Santelices and Varela, 1993a; Santelices et al., 1995, 1996). It has been suggested that genetic changes in vegetative clones of *G. chilensis* are quickly and strongly affected by environmental conditions (Meneses and Santelices, 1999). Thus clonal selection of *Gracilaria* should not only involve isolation of clones with superior characteristics, but also the persistence of selected characteristics (Santelices, 1992). The use of these new conceptual aspects in strain selection programs should help to improve the production of *Gracilaria* and other red algae in the future.

Other studies have shown that the persistent use of the same cultivated area triggers the development of pests that affect *Gracilaria* production (Buschmann et al., 1995, 1999a). Herbivorous fish, gastropods and polychaetes have been mentioned as detrimental to *Gracilaria* production (Pizarro, 1986; Jara, 1990). Although some pesticides may control polychaetes (Briganti, 1992), high mortalities among high-level predators have been linked to the use of such chemicals, indicating negative environmental consequences (Buschmann et al., 1996a). In some areas the appearance of mussel infestations of thalli has affected host growth and facilitated dislodgment of plants due to added weight (Retamales and Buschmann, 1996). So far, experimental evidence supporting methods controlling invertebrates in *Gracilaria* farms is scarce. However, it has been suggested that rotation of farming areas could be a useful strategy in overcoming this problem (Retamales and Buschmann, 1996).

Red, green and brown epiphytic algae can cause severe damage in Chilean *Gracilaria* farms (Pizarro, 1986; González et al., 1993; Buschmann et al., 1995). It has been demonstrated that epiphytism implies lower algal growth rates, increased loss of stocking biomass and that production of raw material with lower economic value due to the presence of the nuisance algae (Kuschel and Buschmann, 1991; Buschmann and Gómez, 1993; Buschmann et al., 1994a). The epiphytic loads signify an increased water drag that causes lower production rates. Several methods have been suggested to control epiphytes, such as physical removal from the host, reduction of light intensity with netting or changing of light quality, drying of culture systems, change in water circulation, preventive chemical methods (e.g., use of hypochlorite solutions) copper based paints, manipulation of pH and nutrient regimes, and biological methods (Fletcher, 1995). Most of these methods are only suitable for tank cultures and are difficult to apply successfully in open culture areas, as is the case for *Gracilaria* in Chile. Recent information indicates that an understanding of recruitment patterns and mechanisms of host infection is useful when selecting management strategies for minimising epiphyte loads in *Gracilaria* farms (Buschmann et al., 1997a, 1998). An alternative approach includes the use of the snail *Tegula atra* as a biological control due to its selective consumption of ceramialean epiphytes (Buschmann et al., 1994a). This approach, however, has not been tested on a commercial scale. *Gracilaria* susceptibility to epiphytes varies among populations (Santelices and Ugarte, 1990; Buschmann et al., 1992), and according to the production of sulfated polysaccharide exudates (Santelices and Varela, 1993b). *Gracilaria* thalli can also be infected by an endophytic amoeba (Correa and Flores, 1995). In the laboratory, *Gracilaria* developed whitish spots which rapidly spread throughout the thallus, but this disease has not been recorded in wild populations or commercial farms in Chile.

Sedimentation has been cited as an important problem in subtidal cultivation systems. Although *Gracilaria* needs to be covered by sand for proper anchoring, an excess of sediment is detrimental as it diminishes light needed for growth (Westermeier et al., 1988b, 1991). The natural process of sand accumulation induced by *Gracilaria* plants is enhanced by the extended use of wooden fences to delimit the planted areas and to capture drifting algae, a practice that also alters the sedimentation process. Sedimentation dynamics do not appear to have the same influence on production in intertidal farms, but the selection of adequate areas for planting *Gracilaria* can improve production and maintain low loads of herbivorous polychaetes (Buschmann et al., 1997b).

Development of salmon, molluscs and *Gracilaria* farming during the past ten years has severely limited the availability of suitable cultivation areas in southern Chile (Buschmann et al., 1996a). For this reason, efforts are being made to look for alternative technologies. Bravo et al. (1992) suggested that intertidal enclosures could be installed high in the intertidal zone where the tidal regime exchanges seawater twice daily, obtaining 30% higher biomass production than the traditional intertidal farming. Floating cultures of *Gracilaria* can also be integrated with salmon rafts, helping to reduce nutrient load in the surrounding water (Troell et al., 1997). A recent review (Troell et al., 2003) demonstrated that this approach is technically feasible and ready for application, however some research is still needed to optimise results. Tank cultivation of *Gracilaria chilensis* has also been undertaken (Edding et al., 1987; Ugarte and Santelices, 1992) and long term experiments have demonstrated that the initial inoculum can be maintained for at last three years without loss of their productive capacity (Retamales et al., 1994). Nevertheless, this type of culture has not attracted private investors because it is not profitable. To improve profitability, tank cultivation using salmon effluents has been developed (Buschmann et al., 1994b). This system was highly productive (biomass production over 48 wet kg m^{-2} $year^{-1}$), and did not involve additional pumping, nutrient and CO_2 costs. If the *Gracilaria* tank cultures are integrated to a salmon farm, it is possible to reduce the negative impact of fish waste, whereas most of the cost of algae cultivation is then covered by the operational costs of the salmon farm, that results in a economically profitable and ecologically friendly system (Buschmann et al., 1996b). A further advantage is that algae cultivated with fish waste-waters have a higher agar quality (Martínez and Buschmann, 1996). Floating culture systems like those used in Africa and Venezuela (Dawes, 1995) were also experimentally tested in Chile (Pizarro, 1986; Westermeier et al., 1993).

5 Other red seaweeds

Algae belonging to the genus *Gelidium* are the main agarophytes currently exploited commercially in Chile. Species of *Gelidium* typically occur on rocks in the low intertidal zone down to a depth of 25 m, often on coralline crusts and associated with rapid water movement (Santelices, 1991). Several of these species have been studied to assess their potential for cultivation in free-floating or net culture systems (Santelices, 1987). *Gelidium lingulatum* for which demand is highest, showed that net cultures installed in intertidal gullies and rapids can reach daily growth rates as high as 3% at intertidal levels of 0.4–0.8 m above mean low water level. The effect of environmental factors on *Gelidium* species can be found in Correa et al. (1985). More recently, Rojas et al. (1996) successfully induced the reattachment of *Gelidium rex* to scallop shells, producing 1.5 cm plantlets in 40 days. Nevertheless, market conditions do not favour a higher demand for other agarophytes.

Compared to agarophytes, demand for carrageenophytic seaweeds in Chile has increased in recent years, as a result of the establishment of processing plants that extract the colloid. However, the supply of these species relies on the harvesting of wild stocks. Following the experience gained with *Gracilaria*, several studies have reported results on basic biological and ecological aspects for several carrageenophytes exploited in Chile. For example, studies on population ecology and reproduction (Martínez and Santelices, 1992; Santelices and Martínez, 1997), biotic interactions (Jara and Moreno, 1984; Hannach and Santelices, 1985; Buschmann and Santelices, 1987; Buschmann and Vergara, 1993), diseases (Correa et al., 1997; Buschmann et al., 1997c) and recommendations for population management of wild stocks (Santelices and Norambuena, 1987; Westermeier et al., 1987; Gómez and Westermeier, 1991), are available for *Mazzaella laminarioides*. However, studies directly related to mariculture are lacking.

Other algae like *Sarcothalia crispata* and *Gigartina skottsbergii* are much less studied, but several research groups are currently working on the development of mariculture strategies and techniques for these species. *Sarcothalia crispata* (Figure 2(b)) is today one of the most demanded red algae for carrageenan extraction in Chile (Figure 14). Population studies of this species show a marked variation in abundance, with maximum densities around 2,000 fronds per square metre in late spring and maximum biomass of 1.2 wet kg per square metre in summer (Avila et al., 1996). Available information suggests that the abundance of this alga depends on recruitment from spores and not on the regeneration capacity of the holdfast (Mora, 1992). Laboratory experiments with *Sarcothalia crispata* determined a suitable combination of environmental factors (temperature, salinity, light intensity, photoperiod and macronutrients) to optimise seeding of artificial substrata (different types of ropes and rocks). In the laboratory, temperature and irradiance can be manipulated for increasing the growth and survival responses of *S. crispata* (Avila et al., 2003a). Transplanting these laboratory-produced sporelings has had limited success, with survival rates below 40% after two months in the field (Avila et al., 1995). Avila et al. (1999a) presented results of studies where frames with nylon and polyfilament of different diameters were seeded in the laboratory and later out-planted to the sea. These authors indicate that a total output of 140 g (dry weight) m^{-2} can be obtained over the growth period (November–May).

Figure 14 Foreign researchers inspecting *Sarcothalia crispata* in Chile

Gigartina skottsbergii is another species subject to intensive research, in particular due to the quantity and quality of its carrageen content (Buschmann et al., 1999a). A population study of *G. skottsbergii* demonstrated that in Chile this species shows a higher gametophytic abundance during autumn-winter, associated with low temperatures and short-day conditions (Zamorano and Westermeier, 1996; Westermeier et al., 1999). This abundance pattern is similar to that found in southern Argentina (Piriz, 1996), where it has also been shown that the most abundant standing stocks develop from spring to late summer, with values around 300 g (dry weight) m^{-2}. The reproduction effort is concentrated in winter and early spring, as observed in high carpospore and tetraspore abundance in laboratory experiments (Avila et al., 1999b). However, other laboratory experiments with *Gigartina skottsbergii* presented a clear seasonal pattern of successful germination, with the highest value of 50% recorded for winter spores (July and August) (Buschmann et al., 1999b, 2001b). Better germination results were obtained at 5°C than at 10°C or 15°C (Buschmann et al., 1999b). These results do not fit with previous data obtained with plants collected in the Antarctic (Bischoff and Wiencke, 1996). Germlings smaller than 500 μm have been transplanted from a nursery to outdoor tanks, where their survival was higher than 80% with growth of up to 1–2 mm in 30–45 days. Light, temperature and other environmental factors affecting its growth have been established recently (Buschmann et al., 2004a). To date hatchery-produced *Gigartina* germlings have not been reported, although spore seeded substrata have been successfully transplanted into the sea (Avila et al., 2003b). This evidence emphasizes two bottlenecks for the future development of *Gigartina* mariculture. First, lack of seasonal spore availability, and second, low germination and growth potential. For this reason, efforts have been made to propagate this species through the production of protoplasts and vegetatively in laboratory and field conditions (Buschmann et al., 2001b). These results encouraged further experiments in nurseries, which have shown that frond fragmentation is technically feasible and that healing and regeneration responses can be optimised by experimental manipulation of temperature, light and nutrient concentrations (Correa et al., 1999). Explants of *Gigartina* fronds have also been cultivated in floating ropes in southern Chile, demonstrating that they can regenerate and have surface increments of 90–250% over a 6-month period during summer (Buschmann et al., 1999b). Other forms of vegetative propagation are also being explored. The use of rhizoids attached to rocks and transplanted to the sea could be an interesting possibility that requires further research (Buschmann et al., 2001b). Cultivation seems one form of restoring these populations in southern Chile and because of their genetic uniqueness a priority should be given to the preservation of the species genetic pools (Faugeron et al., 2004), whereas care must be taken when strain selection programs are developed to achieve higher production levels. The main restriction to further development of *Gigartina* is its low growth potential. It is important to assess the plant growth potential to enhance production when developing a strain selection program (Buschmann et al., 2001b). In this context, growth rate and production potential in *Gigartina* require further attention but it seems that the development of a strain selection program is unavoidable. Vegetative propagation of this species is feasible, a feature which should contribute greatly to the establishment of such a program. As part of this strategy, research is underway to obtain higher growth rates (Buschmann et al., 2001a).

Edible seaweed commercialisation is also growing in Chile. *Porphyra columbina* has being exploited by coastal communities since ancient times. Population studies on *P. columbina* show that maximum abundance occurs in spring. This pattern is modified in the lower intertidal zone by competition with *Mazzaella laminarioides* and by grazing (Santelices and Avila, 1986). Factors that regulate *P. columbina* life-history have been established (Avila et al., 1986), and at least one study has demonstrated that cultivation of this species is biologically feasible (Seguel and Santelices, 1988). Nevertheless, the limited local market is not sufficiently attractive to stimulate the investment required for its cultivation on a commercial scale. Interestingly it has been recently indicated that not only *P. columbina* exist in Chile, but also other commercially more interesting species such as *P. linearis, P. pseudolinearis, P. miniata, P. capensis, P. woolhousiae, P. lanceolata, P. torta* and *P. thuretii* (González and Santelices, 2003), thus attracting new perspectives for *Porphyra* cultivation in Chile.

During the last years, a market has opened in Chile for *Callophyllis variegata* and *Chondracanthus chamissoi*. Knowledge on these species was restricted to distribution data (Hoffmann and Santelices, 1997), although some information regarding phenology and spore handling in laboratory is now available for *C. chamissoi* (González and Meneses, 1996; Bulboa and Macchiavello, 2001). Spore-propagation in natural beds is an important mechanism to explain seasonal biomass regeneration of *C. chamissoi* (Macchiavello et al., 2003). In *Callophyllis variegata,* carpospores are available during winter, whereas tetraspores are available during spring (Güttler, 2000). Furthermore, natural populations of *C. variegata* are also being studied to develop management recommendations. From this perspective, it has been demonstrated that this species holdfasts show a high regeneration capacity, which enables recovery of the harvested population. However, care must be taken when identifying *Callophyllis variegata* as it coexists with several morphologically very similar undescribed species.

6 Conclusions

The Chilean seaweed industry has diversified significantly over the last years. The number of species being commercialised and processed has increased. Important highlights are the development of the carrageenan industry, the increased production of agar, the increasing interest for brown algae and the addition to Chilean exports of highly valuable species such as the edible seaweed *Callophyllis variegata*. Additionally, the development of new products, such as organic fertilisers or novel food products, is adding an increasing economical return to the country. In spite of the above achievements, *Gracilaria chilensis* remains the only commercially cultivated species, a situation that is expected to change in the near future. Tank culture of *Gracilaria* has not been developed on a commercial scale, although efforts are being made to develop integrated land-based fish, mollusc and seaweed farming systems (Figure 15, Buschmann et al., 1996b, 2001c; Chopin et al., 2001).

Figure 15 Land-based integrated salmon-oyster-*Gracilaria* tank culture system in southern Chile

An analysis of the knowledge accumulated on other exploited red and brown algae, indicates that an important amount of studies are essential for the development of mariculture (Table 1). However information on ecophysiological characteristics of Chilean seaweeds has increased significantly during the past years (Table 2), but greater collaboration between the scientific community and industry may help in the future (Santelices, 1996). In this context, it is important to mention that some research groups are developing different approaches for the management and cultivation of several economically important Chilean seaweeds whereas some companies have become involved in these efforts (Marín et al., 2002). This trend should be seen as an important complement to government agencies that currently support basic and applied phycological research in Chile, and will likely result in a greater diversification of farmed species in coming years (Santelices, 1999).

Table 1 Summary of applied studies (experimental and pilot scale) of commercially important: (a) red and (b) brown algal species in Chile

Species	*Population dynamics*	*Laboratory cultures*	*Nursery studies*	*Tank cultivation*	*Suspended cultivation*	*Bottom cultivation*	*Pest control*
A. Red seaweed							
G. chilensis	**	**	**	**	**	**	*
Gelidium spp.	**	*	–	*	*	–	–
M. laminariodes	**	**	–	–	–	–	*
S. crispata	**	*	**	*	*	–	*
G. skottsbergii	**	*	**	–	*	–	*
C. chamissoi	*	**	*	–	–	–	–
G. furcellatus	*	*	–	–	–	–	–
P. columbina	**	**	*	*	*	–	–
C. variegata	*	*	*	–	–	–	–
B. Brown seaweeds							
M. pyrifera	**	**	**	*	*	–	–
M. integrifolia	*	*	*	–	–	–	–
L. nigrescens	**	**	*	–	*	–	–
L. trabeculata	*	*	*	–	*	–	–
D. antarctica	*	*	–	–	–	–	–

*Incomplete information.

**Complete information available.

– Information not available.

Source: Modified from Buschmann et al. (2001a)

Table 2 Summary of some ecophysiological available data on commercially important algal species in Chile

Species	Optimal growth conditions: Temperature (ºC)	Irradiance (μ mol $m^{-2}s^{-1}$)	Age	Phase	Condition	Photosynthetic parameters: α	I_k	Age	Phase	Condition	References
Callophyllis variegata	8[a]	12[a]	Re-growth[a]	Sporophyte[a]	Lab[a]	0,14[b]	181,7[b]	Adult[b]	Unknown[b]	Lab[b]	[a]Muñoz et al. (2004) and [b]Gómez et al. (2004)
Chondracanthus chamissoi	25	70	Adult	Gametophyte and sporophyte	Lab	–	–	–	–	–	Bulboa and Macchiavello (2001)
Gelidium lingulatum	15[a] 15–20[b]	120[a] 25–75[b]	Juveniles[a,b]	Gametophyte[a,b]	Lab[a,b]	0.34[c]	335.6[c]	Adult[c]	Unknown[c]	Lab[c]	[a]Oliger and Santelices (1981), [b]Correa et al. (1985) and [c]Gómez et al. (2004)
Gigartina skottsbergii	0[a] 11–12[b]	–	Juveniles[a,b]	Unknown[a,b]	Lab[a]	0.481[c] 0.431[d]	85.3[c] 62.1[d]	Adult[c,d]	Sporophyte[c] unknown[d]	Lab 15[c] 12[d]	[a]Bischoff and Wiencke (1996)[b,d]Buschmann et al. (2004) and [c]Wiencke et al. (1993)
Gracilaria	15[a] 25[b]	20–50[b]	Adult[a,b]	Unknown[a,b]	Lab[a,b]	0.15[c]	182.8[c]	Adult[c]	Unknown[c]	Lab[c]	[a]McLachlan and Bird (1984), [b]Pizarro (1986) and [c]Gómez et al. (2004)
Lessonia nigrescens	14[a] 5–10[b]	50[a] 25–100[b]	Juveniles[a,b]	Sporophyte[a,b]	Lab[a,b]	–	–	–	–	–	[a]Hoffmann et al. (1984) and [b]Avila et al. (1985)
Macrocistys pyrifera	–	–	–	–	–	0.22[c] 0.016[d]	327.4[c] 141[d]	Adult[c,d]	sporophyte[c,d]	Lab[a] Environm[b]	[c]Gómez et al. (2004) and [d]Gerard (1986)
Mazzaella laminarioides	10–15[a] 15[b]	50[a] 60[b]	Adult[a] sporling[b]	Gametophyte[a] both[b]	Lab[a,b]	0.06[c]	237.2c	Adult[c]	Unknown[c]	Lab[c]	[a]Wiencke and Dieck (1990), [b]Hannach and Santelices (1985) and [c]Gómez et al. (2004)
Porphyra columbina	10–15[a] 15[b]	50[a,b]	Adult[a,b]	Gametophyte[a] conchocelis[b]	Lab[a,b]	0.2[c]	136.5[c]	Adult[c]	Gametophyte[c]	Lab[c]	[a]Avila et al. (1986) and [b]Gómez et al. (2004)
Sarcothalia crispata	15[a,b]	60[a] 30–50[b]	Juveniles[a,b]	Gametophyte and sporophyte[a,b]	Lab[a,b]	0.13[c]	181.7[c]	Adult[c]	Unknown[c]	Lab[c]	[a]Romo et al. (2001), [b]Avila et al. (2003a, 2003b) and [c]Gómez et al. (2004)

α: Photosynthetic efficiency.
I_k: Photosynthetic saturation irradiance.
–: Data non available.

Acknowledgements

The authors greatly acknowledge the financial support of FONDECYT (Grant No. 1010706) and FONDEF (Grant No. D01I1151). The help and support of R. Espinoza, V. Muñoz, C. Moreno, L Henríquez, G. Aroca and C. Astudillo, among others, is sincerely appreciated. Many ideas presented in this paper have been discussed with Alfonso Gutiérrez and the manuscript was significantly improved by Robert Stead.

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