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The status of research and utilisation on the subtidal kelp along the Chilean coast: A literature review

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Abstract

The most important marine coastal ecosystem in the Chilean coast are kelp forests. This review is based on ecological studies regarding different aspects of subtidal kelp ecosystems along the Chilean coast. It highlights the most interesting findings in (1) biology of subtidal kelp in Chile, with particular reference to (2) habitats formed by kelp, and considered the successful examples and promising results in the (3) kelp as an industrial resource (Biotechnological approach of kelps and aquaculture). The impact caused by (4) El Niño-Southern Oscillation is discussed as an important climatic event that could help to forecast the future of the kelp ecosystem. In addition, this literature review outlines the knowledge gaps on subtidal kelp along the Southeast Pacific Coast of Chile, so that research can be strengthened in the future.

Key words: kelp, macroalgae, harvesting, commercial kelp, subtidal, SE Pacific Ocean

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1 Introduction

Kelp, large brown macroalgae in the order Laminariales, is considered as one of the most important marine foundation species forming habitats that account for 43% of global ecoregions, the biogeographic areas of homogeneous species compositions that is distinct from an adjacent ecological system (Spalding et al., 2007; Krumhansl et al., 2016). The goods and services of extensive kelp ecosystems share a great part in the global economy. Depending on a country of kelp source, 1 km^2 of kelp can be worth from 500 000 $US (South Africa) to 800 000 $US (Chile), and to 1 000 000 $US (Australia). These numbers refer to the market price of kelp as food and as raw material for the extraction of its natural compounds, as well as its ecological value as habitat provision, shelter and direct food for marine species, coastal protection and carbon storage (Wernberg et al., 2013; Vásquez et al., 2014; Bennett et al., 2016; Blamey and Bolton, 2018). However, this monetary tag of kelp goods and services is very likely to be underestimated due to the lack of in-depth studies. The real number could be up to six times greater when the indirect uses of kelp services are included (Filbee-Dexter and Wernberg, 2018).

Nowadays, most of the natural ecosystems, such as seagrasses, mangroves, corals are under threat or declining (Pandolfi et al., 2003; Waycott et al., 2009; Goldberg et al., 2020). Around 38% of documented kelp habitats worldwide are on a negative regression line, overweighting the stable or increasing kelp biomass in other areas, which results in a global average decline of 1.8% per year (Krumhansl et al., 2016). There are three main factors altering kelp forests worldwide: overfishing, kelp overexploitation, and climate change (Ortiz et al., 2013; Smale and Wernberg, 2013; Vergés et al., 2014). Overfishing of high-trophic level species, such as Chilean sandperch (*Pinguipes chilensis*), Peruvian morwong (*Cheilodactylus variegatus*) or *Graus nigra*, that prey on various grazers, including sea urchins, affects the kelp populations indirectly, following the top-down ecosystem control: overfishing that removes the predators of sea urchins from the ecosystem, which are the most conspicuous kelp grazers. Without predators the sea urchins increase in numbers and their feeding on kelp leaves extensive barren grounds (Steneck et al., 2002; Filbee-Dexter and Scheibling, 2014). In addition to this, kelp is harvested for the extraction of phycocolloids for alginate production (Augier and Santimone, 1978; North, 1979; Vasquez and McPeak, 1998) which is an important export good in Chile. Furthermore, kelp is also harvested for direct food consumption of its soft parts (for soups, sushi, etc.), popular in East Asian cuisine (Chapman and Chapman, 1980; Abbott, 1996; McHugh, 2003). However, one of the greatest kelp habitats loss worldwide is considered to be caused by global warming and heatwaves (McHugh, 2003; Schiel et al., 2004; Vega et al., 2005; Wernberg et al., 2013; Oliver et al., 2018; Arafeh-Dalmau et al., 2019, 2020). Moreover, warming ocean allows warm-water species to expand their habitats, and thus, kelp may be affected by herbivorous newcomers and, could eventually be replaced by structurally much simpler turf algae mats, as has been observed along the western coast of Australia (Smale and Wernberg, 2013; Filbee-Dexter et al., 2016; Wernberg et al., 2016; Arafeh-Dalmau et al., 2019, 2020). Although a large percentage of kelp habitats are lost globally, yet in almost 27% of

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world ecoregions kelp growth is increasing and in 35% ecoregions no alteration has been observed. This suggests that besides the global drivers, such as climate change, the local stressors play a significant role in kelp population dynamics (Krumhansl et al., 2016).

Kelp is one of the most important natural resources in Chile, accounted to have a value of 541×10^6 $US, which can be broken into 75% of kelp harvesting for biocompound extraction, 15% of fisheries, 4.8% of scientific interest and 4% of biodiversity and climate buffer as well as cultural heritage (Vásquez et al., 2014). Due to the cold Humboldt Current and rocky substrate, kelp habitats form on the entire western coast of South America, from Peru to Argentina (Graham et al., 2007; Thiel et al., 2007; Pérez-Matus et al., 2017). As there are neither coral reefs, nor abundant seagrass meadows, nor mangrove forests observed on the Chilean coastline, kelps are the main species forming complex three-dimensional marine habitats (Christie et al., 2003; Vásquez et al., 2014). Subtidal species, *Macrocystis pyrifera* and *Lessonia trabeculata*, have been less actively studied than intertidal species, perhaps due to higher logistics costs limiting subtidal research in general (Ban, 2009). Nevertheless, subtidal kelps are the ones that form standing kelp forests—an ecosystem hosting an invaluable variety of marine creatures (Mann, 1973; Steneck et al., 2002; Wernberg and Filbee-Dexter, 2019).

In this review, the aim is to provide extensive state-of-the-art information on subtidal kelp research in Chile based on literature analysis, emphasising the most significant research outcomes and persisting questions. It is important to add the latest research findings achieved in the last decade, thus updating the previous reviews on the kelp research. Furthermore, to our knowledge, this is the only review that focuses exclusively on subtidal kelp species along the Chilean shore, which borders with natural kelp growth in all its extension. The following topics are addressed in this review: biology of subtidal kelp in Chile; habitats formed by kelp; kelp as an industrial resource (biotechnology approach to kelp and aquaculture); and effects of El Niño-Southern Oscillation (ENSO). We finished this review with conclusions and research gaps that we hope can be addressed in the future works.

2 Materials and methods

This study compiles 36 scientific papers on the topic of Chilean kelp, the list which is provided in the Supplementary information. The scientific literature consisted of primary sources available online in ScienceDirect, PubMed, Google Scholar, and Mendeley databases, with a special focus on peer-reviewed journals from 1975 to 2020 though some older relevant papers were also examined. The keywords used in the search criteria included: "subtidal kelps" OR "*Macrocystis pyrifera*" OR "*Lessonia trabeculata*" OR "subtidal kelp ecosystem" OR "kelp biotechnology" OR "kelp research" OR "kelp aquaculture" OR "kelp harvest" AND "Chile". All the information was then contrasted and summarised. Additionally, the persisting research gaps have been listed in the discussion section of this review.

3 Results

There were 36 peer-reviewed articles found that were relevant for this review. The articles in which the subtidal kelp was not the subject of focus or was not investigated separately (e.g., beach wrack of both subtidal and intertidal kelp species) were excluded from further analysis. The oldest scientific papers included in this review date back to the 1980s: Castilla and Moreno (1982); Moreno and Sutherland (1982); Ojeda and Santelices (1984); Dayton (1985). These works were included in this review as the findings which paved the further advancement in knowledge that has been achieved to date. Only two articles written in the 1990s were relevant to our review topic. The greatest knowledge was generated during the last two decades (30 articles). *Macrocystis pyrifera* kelp has been notably of a greater scientific focus than the other subtidal species *L. trabeculata*, as our search found only 2 articles dedicated to endemic *L. trabeculata* kelp (Fig. 1).

3.1 *Biology of subtidal kelps in Chile*

The temperatures of Chilean coastal waters vary from north to south, sea surface temperature reaching over 20℃ in the north and below 5℃ in the south (Tala et al., 2016). The coastline is dominated by the Antarctic Circumpolar Current, which breaks into the Humboldt Current flowing up-north and the Cape Horn Current passing by the southernmost tip of Chile (Thiel et al., 2007; Camus, 2001). The dominant Humboldt Current is characterised by continuous upwelling, which brings nutrient-rich waters to northern Chile. Rather more seasonal upwellings occur in southern parts of Thiel et al. (2007). Furthermore, this cold-water current system reduces air temperature, and inhibits precipitation, creating a dry and cold climate with nutrient-enriched coastal waters (Rutllant, 2003). Due to local geographic differences producing localised eddies and current circulations, the

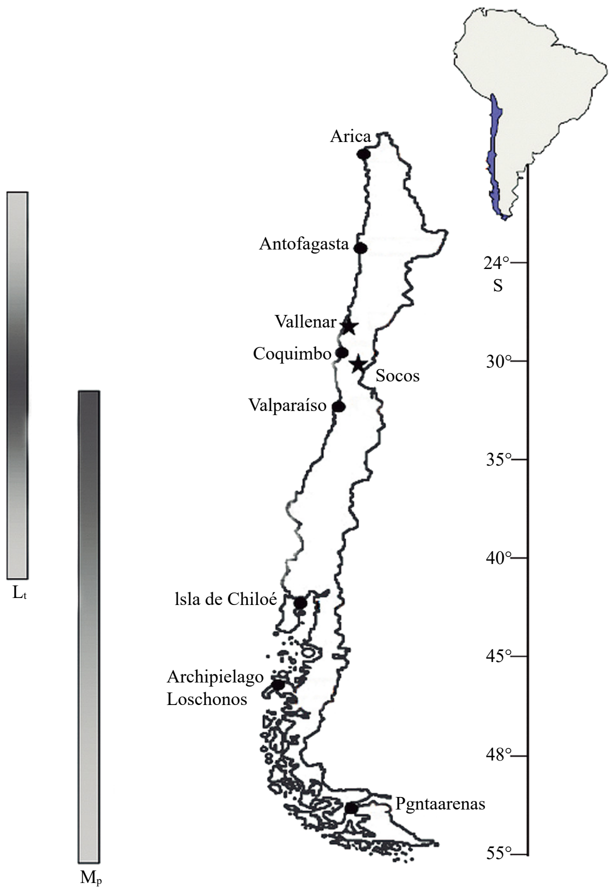

Fig. 1. Map of Chile and country's location in South American continent, showing geographic distribution of subtidal kelp species (grey bars), *Lessonia trabeculata* (L_t) and *Macrocystis pyrifera* (M_p). The sites marked on the map depict the main kelp harvest and process of raw material sites (dots) and the main distribution hubs (stars). Adapted from Vásquez (2008).

Chilean coast is considered highly heterogeneous, creating various niches for a wide variety of species (Thiel et al., 2007). Types of kelps (Order Laminariales) found in Chile are *L. nigrescens*, *L. berteroana*, *L. spicata*, *L. trabeculata*, and *M. pyrifera*, and the fucoid *Durvillaea antarctica*, which is not true kelp, but because of its honeycomb-like inner structure filled with gas, thus positively buoyant, is studied as a species of kelp (Fraser et al., 2012; Vásquez, 2016 and the references therein). In Chilean waters, kelp grow from the intertidal areas up to around 30 m depth (Vásquez, 2016). Only two species are exclusively subtidal, *M. pyrifera* and *L. trabeculata*, yet expressing distinct distribution patterns, both along the depth gradient and geographic latitude (Table 1). The first one is the dominant kelp south from 42°S (Chiloé region), and the second one dominates from central up to the northern coast (18°–42°S) and is an endemic species with no other records of distribution outside Chile (Vasquez, 1992; Hoffmann and Santelices, 1997; Vásquez and Buschmann, 1997; Tala et al., 2004; Ramirez et al., 2008; González et al., 2012).

3.2 *Habitats formed by kelp*

In this subsection, the habitats formed by kelp are divided into three groups: standing kelp forests; surface floating canopy; and detached parts forming rafts (Fig. 2). It is worth noting that kelp wrack provides another niche for various foraging organisms. The macroalgae wrack washed ashore is a direct food, as well as shelter for various upper and lower beach inhabitants (amphipods, isopods, tenebrionids) (Jaramillo et al., 2006; Duarte et al., 2010; Quintanilla-Ahumada et al., 2018). However, it seems that so far only intertidal, or macroalgae wrack of mixed species from intertidal and subtidal habitats has been researched and, to our knowledge, no research focusing entirely on the subtidal kelp wrack and the associated organisms has been published to date. Furthermore, there is little attention paid to benthic microhabitats, (i.e., assemblages of algae and associated organisms formed under the canopy of the attached kelps). It is known that there are macroalgae communities associated and dependent on *M. pyrifera* abundance, although the species traits (competition vs. habitat provision) still must be explained further (Almanza and Buschmann, 2013). In addition, no research in Chile, to our knowledge, considered kelp holobionts (i.e., assemblages of microorganisms) which are, very likely, even vital for the macroalgae survival, as it has been explained by the study of Michelou et al. (2013) in *M. pyrifera* specimens from California, USA. Thus, due to the lack of research on these topics in the Southeast Pacific region, the kelp wrack, understorey habitats and kelp holobionts are not described in this review. Environmental heterogeneity provided by kelp is mostly focused on large and medium scales, yet even shifts underpinned in micro-scales can be of utmost importance for meiofauna and small macrofauna-size communities, and therefore should not be overlooked (Shelamoff et al., 2019).

Table 1. Subtidal kelp species distribution in Chile

Species	Area	Distribution	Resource
Macrocystis pyrifera	dominant species from Chiloé region to Magellan Strait	shallow subtidal to 10 m	Dayton (1973); Palacios and Mansilla (2003); Plana et al. (2007); Camus et al. (2021)
Lessonia trabeculata	dominant from border with Peru to Chiloé region	shallow subtidal to ca. 30 m	Vásquez (2008)

Note: ca., abbreviation for circa.

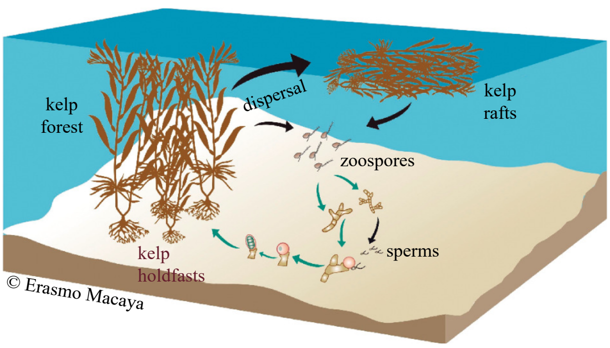

Fig. 2. Schematic view of habitats formed by kelp *Macrocystis pyrifera*: holdfast, standing kelp forest and kelp rafts. Drawing adapted with permission of the author (Erasmo C. Macaya).

Macrocystis pyrifera is the dominant subtidal kelp in central and southern Chile, with the exception of the Patagonia region (Vásquez, 2016; Mora-Soto et al., 2020). In this area, there are two growth and reproduction patterns of *M. pyrifera* identified (Buschmann et al., 2004): (1) the kelp population is reproductive throughout the year but only in exposed areas; and (2) in sheltered areas, reproduction starts in late winter, having fertile sporophytes in summer-autumn and completely degrading afterwards. *Macrocystis pyrifera*, an underwater forest forming kelp, has been studied as an important habitat for many bivalves, annelids, isopods, peracarids, nudibranchs, chitons, gastropods, decapods, amphipods and crustaceans, and their predators such as the asteroid *Diplasterias brandti*, or the juvenile crabs *Lithodes antarctica*, as well as spawning grounds for Patagonian squid *Doryteuthis gahi* (Santelices and Ojeda, 1984; Cárdenas et al., 2007; Hinojosa et al., 2007, 2010; Wichmann et al., 2012; Rosenfeld et al., 2014).

The main kelp grazers found on the Chilean coast are the marine snail *Tegula tridentata*, the sea urchins *Loxechinus albus*, *Tetrapygus niger* and asteroid *Heliaster helianthus* (Vásquez and Buschmann, 1997; Pérez-Matus et al., 2017). These herbivorous species are identified as keystone species in the Southeast Pacific kelp forests as their abundance affects the resilience of the whole ecosystem (Ortiz et al., 2013; Hermosillo-Núñez, 2020). The closer observations of the effects of sea urchins (one of the most voracious keystone species and kelp grazers), showed very different effect of the dynamics of these echinoderms on kelp habitats along the Chilean coastline as compared to their effect on kelp forest ecosystems along the North American coastline. In California, sea urchins have overgrazed extensive *M. pyrifera* forests in the past, leaving barren grounds and thus drastically altering the whole coastal ecosystem (Lawrence, 1975; Dayton et al., 1992; Graham, 2004). On the other hand, the investigations conducted along the coastline of South American, mainly Chile, showed only mild effects of kelp grazing by sea urchins (Castilla and Moreno, 1982; Moreno and Sutherland, 1982). The lack of negative impact of the grazing of sea urchins was explained by Vásquez et al. (1984) and Dayton (1985), who collected data from oceanographic observations, sea urchin recruitment patterns, human interference, and experimental studies and suggested that *M. pyrifera* growth and densities in Chile are affected by multiple factors which differ according to the geographic location. The westwind drift current and exposure to strong wave surges, mostly pronounced in southern Chile, greatly limit the sea urchin larvae recruitment, so the dense areas of *M. pyrifera* forests can flourish (Dayton, 1985). Moreover, sea urchins are collected by the local fishermen at some locations, which is another factor reducing the population of this echinoderm. Hence, in areas where larvae settlement is easier, sea urchin populations negatively correlate with *M. pyrifera* densities (Vásquez et al., 1984; Dayton, 1985). Thirty-five years later, Hermosillo-Núñez (2020) brought back the topic of conspicuous echinoderm species relation to kelp forests, investigating in detail the northern Chilean coastal region. The study analysed a broad variety of the main macro invertebrates and their trophic relations, and added more herbivorous and carnivorous echinoderms to the list of keystone species in the kelp forest ecosystem. The author highlighted the importance of the balanced presence of echinoderms in the kelp ecosystem and pointed out the anthropogenic stressors, e.g., intensive kelp harvest, as the most probable cause of altered keystone species complex that may result in kelp ecosystem disruption and, eventually, emerging barren grounds.

The research conducted by Pérez-Matus et al. (2007) on the density of kelp and the understorey canopy diversity (microhabitat) and the associated fish showed that denser kelp community and greater variability of understorey species of seaweed facilitates a more suitable environment for species richness and abundance of fish, including economically valuable species like red cusk-eel, *Genypterus chilensis.* Furthermore, the kelp habitat that is composed of both, *M. pyrifera* and *L. trabeculata*, exhibits higher numbers of fish than ecosystems of solitary kelp species (Pérez-Matus et al., 2007). The latter authors also observed that habitat variability depends on seasonal changes on a local scale, which is not detectable on a regional scale. This suggests that the northern coast of Chile can be characterised as highly heterogeneous in terms of nutrients and primary production. Formerly, Camus and Ojeda (1992) had also observed a high heterogeneity of the *L. trabeculata* habitat in northern Chile. Vega et al. (2005) described a mixed kelp species habitat of *M. integrifolia* and *L. trabeculata* at Caleta Constitución, northern Chile. These authors detected that interspecific competition, as well as morphological and physiological adaptation features, influence the morphology of the sporophytes and the distribution patterns of kelp. Nevertheless, the investigations of microhabitats, as well as the habitats formed by mixed kelp species are purely observational, and, to our knowledge, there is a lack of *in situ* experimental work.

Pérez-Matus et al. (2017) compared the abundance of kelp *L. trabeculata* with the fishing pressure in upwelling zones vs. adjacent no upwelling zones. The findings concluded that in the upwelling regions, the density, foliage, and recruitment are significantly higher than in the upwelling unaffected areas, regardless of the fishing regulation. This might be due to the fact that the upwelling zones are hard to access for fishermen, and also that the strong wave actions are likely to move the larvae, preventing an abundant settlement of herbivorous species. Furthermore, in upwelling unaffected sites, the abundance of herbivory species is much higher where their predators are removed by the uncontrolled fishery. This leads to a concomitant consequence, which is the overgrazing of the foundation species–kelps. In the areas where fishing is managed, the biomass of predatory fish is significantly greater and the top-down trophic regulation is enhanced, showing a higher abundance of kelp, fish, benthic carnivores and sessile species. The research concludes that the upwelling events along the Chilean coast induce the bottom-up trophic levels, and fishing is the factor significantly affecting a top-down community regulation and, as a consequence, species richness and abundance.

Kelp, including *M. pyrifera* and *L. trabeculata*, is known to fuse the holdfast and form a coalescence which undergoes morphological changes at cell level. The coalescent algae exhibit notably larger holdfasts or longer thalli, or a higher number of stripes (Wernberg, 2005; Segovia et al., 2014; González et al., 2015). This fusion can be observed also in non-phylogenetically related species (González et al., 2014, 2015). The holdfast coalescent forms more often in the wave-exposed areas, thus, it is believed that such grafting helps to reduce the detachment of the macroalgae (Wernberg, 2005). Ojeda and Santelices (1984) described species richness and temporal variation of kelp associating benthic invertebrates in southern Chile. The study discovered the community structure and dynamics along with the growing habitat—holdfasts, finding that the young and small holdfasts are rapidly occupied by new species but not the large ones, where the species turnover is close to zero. Furthermore, the arrival of new species along the growing holdfasts does not influence the population of earlier inhabitants. This feature contrasts with the colonisation traits in steady or slow-growing habitats, such as seagrass or coral. Various studies have reported significantly higher numbers of epifaunal species inhabiting kelp holdfasts than the canopy (Coyer, 1984; Adami and Gordillo, 1999; Christie et al., 2003; Winkler et al., 2017). The species richness and abundance of epifauna can be significantly lower in fronds than in holdfast areas. Winkler et al. (2017) compared the composition of epifaunal assemblages between fronds and holdfasts of *M. pyrifera* at Punta de Talca, central Chile. In their work, they also checked the epifaunal abundance fluctuation seasonality. The fronds of kelp *M. pyrifera* were found to host 9 different species of epifauna, while 28 species were found among the holdfasts area. The species abundance was also greater (×(8.35±1.65) times) around holdfasts than at fronds areas, even though the total surface area of kelp foliage is substantially larger than the surface area of holdfasts. There was a strong dominance of species *Limnoria quadripunctata* (Isopoda, 50.6% of relative abundance), Polychaeta (20.7% of relative abundance) and *Aora typica* (Amphipoda, 10.9% of relative abundance) in holdfasts of *M. pyrifera*. In the fronds area, the main species were *Peramphithoe femorata* (Amphipoda, 79.9%) and *Amphoroidea typa* (Isopoda, 9.4%). In Punta de Talca, a 5℃ difference in water temperature between the austral summer and winter, thermocline in spring and summer up to 10 m depth and upwelling occurrence in spring, cause variations in nutrient availability and, consequently, seasonal variations in kelp growth. Due to the seasonal fluctuations in kelp primary production, which is highest in austral summer and lowest in austral autumn and winter, the highest epifaunal species abundance among kelp fronds was found in summer, while at the same time, the epifauna abundance in holdfast area was the lowest. Former studies suggest that in early winter the epifaunal species shift their habitat, migrating from the canopy down to the holdfasts, as the fronds are more vulnerable to abiotic conditions (increased winds and waves) (Thiel and Vásquez, 2000; Christie et al., 2003; Miranda and Thiel, 2008; Gutow et al., 2009). The overall invertebrate diversity along the Chilean coastal waters increases towards the south, negatively correlating with fish predation, which is strong in north-central Chile but weakens towards the south (Pérez-Matus et al., 2007; Rivadeneira et al., 2011; Navarrete et al., 2014). The seasonal variability in kelp epifaunal community in southern waters is more pronounced than in northern and central Chile, likely because the seasonal differences of water temperature, nutrients and hydrodynamic forces are greater at higher latitudes (Adami and Gordillo, 1999; Winkler et al., 2017; Friedlander et al., 2018).

A comparative study of *M. pyrifera*, *D. antarctica* and *L. nigrescens* investigated the physiological kelp reaction to temperature and UV exposure. The study examined the ability of different species of kelp to protect from environmental stress and recuperate after the damage, which is an important knowledge for the predictions of the climate change scenarios. The results showed that these species that normally grow in the environment of water temperature below 16℃ have a mechanism to survive a short-term exposure to temperatures up to 30℃. Kelp rapidly induces soluble phlorotannin compounds and delays the induction of non-soluble phlorotannins. The most interesting part is the different limits of each species to the increase of temperature. The species whose upper part of the fronds tend to be exposed to UV even during high tide (*M. pyrifera* and *D. antarctica*) had higher limits to endure higher temperatures than the species that are exposed during the low tide but completely submerged during high tide (*L. nigrescens*) (Cruces et al., 2013). These adaptation differences of some species could be advantageous for surviving in case of temporary unusually high UV penetration because of the changing climate or weather anomalies.

3.3 *Rafting kelps*

Subtidal kelp populations that form detached free-floating rafts have received extensive attention among ecologists in Chile. Detached kelp free floats with surface currents and thus provides the means of dispersal for many associated species (Waters, 2008; Wichmann et al., 2012). Hinojosa et al. (2010) assessed that detached *M. pyrifera* can accumulate in rafts reaching 1 500 kg/km^2 wet biomass during spring season, and can drop down to wet weight 100–200 kg/km^2 in winter depending on the area, as the floating biomass tends to be higher in outer fjords and areas exposed to the open ocean. Even though detached kelp loses its biomass through time, it continues growing and reproducing while free floating on the surface if the environmental conditions are favourable, (e.g., temperature, solar radiance, and nutrient availability). Experimental studies conducted in the northern, central and southern coast of Chile show the correlation of kelp biomass, water temperature and nutrient availability (Hinojosa et al., 2010, 2011). In the northern coastline of Chile, where the water temperature tends to be higher (13–20℃), the loss of floating biomass was significantly greater than in colder waters (Hinojosa et al., 2010, 2011; Rivadeneira et al., 2011). During the austral summer, rafting kelp shows better persistence in the mid and high latitudes (central and southern coast of Chile), where the water temperature is lower, 9–17℃. Thus, the persistence of floating *M. pyrifera* along the Chilean coast can be associated with the latitude and seasonality (Macaya et al., 2005; Tala et al., 2016). Great biomass and relatively long survival time (70–125 d; Hobday, 2000; Hernández-Carmona et al., 2006) on the sea surface appears to form an entirely new ecosystem. The community shift is observed shortly after the algae detach: benthic and holdfast epifauna flees and the planktonic organisms inhabit the niche (Dayton, 1985). While the vertical kelp hosts a higher proportion of peracarid species and lower proportion of molluscs, the rafting kelp is inhabited with higher numbers of molluscs than peracarids. Additionally, within the mollusc group, there are changes in species composition. The abundance of gastropods decreases significantly, leaving the bivalves as the dominant group (Wichmann et al., 2012). Besides forming a new ecosystem, rafting kelps are one of the most important vectors of species dispersal and connectivity for both, their own kelp population, and their associated epibiont species. Macaya and colleagues measured the abundance of rafting kelp and the kelp that remained attaching to a substrate, and the proportion of sporophylls (reproductive fronds) in each group (Macaya et al., 2005). Their findings state that rafting kelp is able to release viable zoospores, yet the detachment event reduces the reproduction rate when compared to the abundance of the sporophylls in the attached kelp at a nearby location. Nevertheless, detached kelps remain functionally reproductive long enough to be able to disperse the zoospores while floating with surface currents long distances. In their study, the stalked barnacles (*Lepas* spp.) were used as bioindicators of the minimum rafting time, which helped to assess the free-floating persistence time and the distance. In fact, some of the rafting sporophytes were driven several hundred kilometres by the Humboldt Current for at least 21 days (Macaya et al., 2005). Kelp-associated communities are also taking advantage of this moving host in order to spread and occupy new territories. The species that are more widespread among biogeographic regions are the ones that are able to persist, directly develop and recruit on the natal floating kelp (i.e., capable of completing the recruitment cycle within the kelp floating time span) (Wichmann et al., 2012). Hence, the dispersal range of rafting-capable organisms depends on the kelp free-floating persistence facilitated by temperature, solar radiation and nutrient availability as well (Helmuth et al., 1994; Wichmann et al., 2012). As an example, the isopod *Limnoria quadripunctata* is a species that bores into the holdfasts of *M. pyrifera* for dispersal purposes. As *M. pyrifera* grows and drifts along the entire coast of Chile, so does this isopod (Haye et al., 2012). However, increasing global water temperature might become a threatening factor for this raft ecosystem. Rothäusler et al. (2011a) experimented with the exposure to a gradient of temperatures and UV rays, mimicking the natural conditions found along the coastline from the north to the south of Chile. The physiological performance of *M. pyrifera* was recorded to ascertain the rafting persistence. The results showed a significant decrease in carbon content and an increase of carbonic anhydrase enzyme in kelp blades due to increasing water temperature which means the sporophytes are suffering from a thermal shock. As a consequence, the higher water temperatures accelerate the disintegration and sinking of free-floating sporophytes. The experimental conclusions explain the field observations of Macaya et al. (2005), where no free-floating kelp sporophyte was found in the waters >20℃ along the northern coast of Chile (Macaya et al., 2005). Additionally, free-floating kelp is the direct food source for various grazing organisms, and this factor would highly contribute to the group of impacts shortening kelp rafting persistence, although the possible alterations in grazing along with an increasing surface temperature have not been assessed yet (Rothäusler et al., 2009).

3.4 *Kelps as an industrial source*

3.4.1 *Biotechnology approach of kelps*

There is a growing interest in macroalgae for the extraction of alginates, agar, and carrageenan, as well as for the production of fish feed supplements (Buschmann et al., 2014). The chemical compound phlorotannin, together with carbohydrate, lipid, and protein contents of subtidal kelp *M. pyrifera* and two intertidal kelp species, *L. nigrescens* and *D. antarctica*, from Chilean waters, were examined by Olivares-Molina and Fernández (2016). The investigated phlorotannins are the compound known to be able to inhibit the angiotensin I-converting enzyme to treat arterial hypertension, and the *M. pyrifera* showed a promising 86% (on average, expressed as IC_{50}) inhibition effect. Furthermore, the kelp nutritional value (carbohydrate, lipid, and protein content) is of interest to the functional food industry. *Macrocystis pyrifera* is found to contain around 9% of carbohydrates and 6% of proteins, and less than 1% of lipids of dry weight. The results showed *M. pyrifera* has a significantly higher carbohydrate content than other kelp species, as well as a higher protein content. Interestingly, the juvenile *L. nigrescens* exhibited higher levels of chemical compounds than the mature kelp, although other species were not tested in their juvenile stages, which could be a basis for future research (Olivares-Molina and Fernández, 2016). Ortiz et al. (2009) obtained much greater nutritional values, most probably due to different extraction method: 13.2 g of proteins, less than 1 g of lipids and around 75 g of carbohydrates per 100 g of dry *M. pyrifera*, as well as all 20 essential amino acids ranging from 0.8 mg/100 g dry weight to 1.8 mg/100 g dry weight. These values are similar to terrestrial plants, such as vegetables and grains, and thus can be considered as an additional source of food for animal or human consumption. Various species of macroalgae in Chile are cultured for the extraction of bioactive compounds used in the food and cosmetics industry, such as agar-agar (24.886 8 $US/t), carrageenan (14.663 3 $US/t), or propilenglicol (17.741 7 $US/t). However, kelp is the major source for alginates production, summing half part of the total algae product export value (Table 2).

3.4.2 *Aquaculture*

In the last decade, seaweed landing in Chile has surpassed 500 000 t wet weight per year (Zuniga-Jara and Soria-Barreto, 2018). The species *L. trabeculata*, *L. nigrescens*, *M. pyrifera*, *M. integrifolia*, and *D. antarctica* are the potential kelp species for commercial growth in Chile, representing over 80% of the total brown seaweed landings (Buschmann et al., 2014). The most intensively harvested kelp is *Lessonia* species, accounting for 90% of kelp wild harvest. Nevertheless, subtidal species *L. trabeculata* and *M. pyrifera*, are being increasingly harvested algae in Chile for two main reasons: the abalone feed and potential food supplement for farmed fish, and the extractions of natural compounds, such as alginates mentioned in the previous paragraph (North, 1979; Vasquez and McPeak, 1998; Mansilla and Ávila, 2011; Buschmann et al., 2014). In Chile, the exploitation of natural seaweed resources is regulated in order to protect the associated biodiversity, as well as the target species of commercial interest (Rebours et al., 2014). Several management strategies have been implemented during the last two decades, including co-management between fishermen unions and the National Public Administration, using strategies based on biological and ecological data, such as quotas per fishing areas, bans, rotation of harvesting, designation of exclusive artisanal fishing zones and also issuing permits for experimenting in designated areas for scientific purposes (Vásquez, 2008; Zuniga-Jara and Soria-Barreto, 2018; Vásquez et al., 2014). The most common kelp harvesting technique in use is the total removal of kelp units (sporophytes). Yet, according to Borras-Chavez et al. (2012), the most sustainable wild harvesting method would be the partial removal of kelp sporophyte (i.e., removal of all fronds from half of each kelp unit growing on the boulder). This method was compared to two other possible techniques: total removal of *M. pyrifera* sporophytes from an entire site (currently used harvest method), or the total removal of every other sporophyte. During the period of two months, the total removal of kelp from a site triggered no sporophyte recruitment. In contrast, two other methods exhibited a significantly higher recruitment rate even compared to a control area, where no kelp was harvested. To date, kelp farming is more expensive than harvesting wild resources due to their complex reproduction cycle, but the worldwide demand and economical pressure to exploit these marine resources in Chile has been increasing in the last decade (Camus et al., 2019). Nevertheless, the technology is advancing and there have been several attempts to investigate the potential of kelp farming. The conditions for the optimal reproduction of endemic *L. trabeculata* were assessed in northern Chile. Findings suggest that the kelp sporophyte development is strongly influenced by aeration, thus the peak of reproduction success is quite a site and season-specific (Tala et al., 2004). Westermeier et al. (2006) have successfully cultured sporophytes of *L. trabeculata* and *M. pyrifera*, and managed to obtain considerable yields of both kelps after growing in the sea: 14 m length and 80 kg/m line of *M. pyrifera* and 0.25 kg/m of *L. trabeculata* fresh weight within 12 and 6 months, respectively. Macchiavello et al. (2010) experimented with the cultivation techniques which resulted in a maximum frond length of 175 cm in 150 days and 22 kg/m of culture rope, which is well within the average growth limits of naturally growing *M. pyrifera*. Camus et al. (2018) conducted a 3-year *M. pyrifera* study between 2010 and 2013 on the suitability of kelp farming at an industrial scale. The extensive study reviewed the feasibility of kelp culturing in suspended systems using submerged ropes with attached *M. pyrifera* seedlings. The maximum yield (wet weight 20 t/(hm^2·month)) was obtained at the most southern location tested (Quenac) adjacent to a salmon farm (Camus et al., 2018). These are promising findings for reducing the harvest pressure of natural kelp biomass, as the landings reach 350 000 t dry weight per year without satisfying the demand (Vásquez, 2008). According to the assessment of Zuniga-Jara and Soria-Barreto (2018), the farming of *L. trabeculata* species could start yielding a profit after six years, while the cultivation of *M. pyrifera* at a large scale could already start yielding a profit after the first year (Correa et al., 2016), thus kelp farming could become an attractive opportunity for a private investor.

Table 2. Natural compounds found in kelps, their production in Chile (in tonnes per year) and export values in 2013. Information source: IFOP and Aduanas de Chile (Jeraldo, 2014)

Compound	Production/t	Value/($US·t^{-1})
Sodium alginate	265.4	14 365.7
Alginic acid	25.4	12 468.5
Potassium alginate	40.1	15 071.9
Magnesium alginate	4	21 850
Total alginates	334.9	**63 756.4**
Other algae compounds	7.6	57 291.8

Note: Total value of alginates is marked in bold.

3.5 *The effects of ENSO*

Due to atmospheric pressure changes, the dry South American coast can experience unusually high precipitation levels, and the warm water flow from Southeast Asia. This phenomenon is called ENSO and it occurs every 3–10 years in the southeastern Pacific Ocean (Gelpke, 2017).

Vega et al. (2005) looked into the effect of ENSO—abnormally higher seawater temperature—on two kelp species, *L. trabeculata* and *M. integrifolia*. The warmer water temperature period was followed by an abnormally cold-water period—La Niña. The two kelp species reacted differently to oscillating temperatures (Fig. 3). During ENSO, the adult sporophytes of *M. integrifolia* showed an increase of abundances, although the juvenile sporophytes did not exhibit any significant changes in growth. When the temperature dropped significantly (1999–2000 La Niña peri-

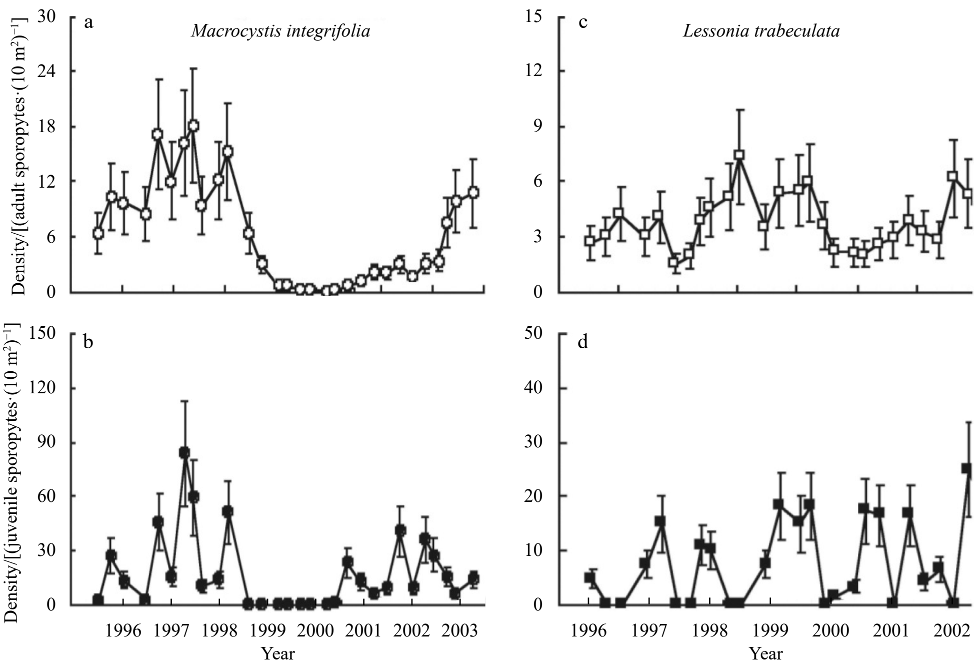

Fig. 3. Density (mean±SE) of adult and juvenile kelp individuals of *Macrocystis pyrifera* and *Lessonia trabeculata* species before (1996), during (1997–1998), after (1999–2003) the ENSO event (Vega et al., 2005).

od), both adult and juvenile sporophytes drastically decreased in abundance. However, *L. trabeculata* responded differently. ENSO had a negative effect on the abundance of *L. trabeculata*, whereas La Niña temperatures favoured the growth of the kelp. The effect of ENSO seems to be significantly greater for juvenile sporophytes than for adult kelp. Nevertheless, the authors stated that the abundance patterns of *M. integrifolia* and *L. trabeculata* did not change drastically during the ENSO event in 1997–1998. The mild effect of ENSO in the study area could be explained by the constant upwelling, which cools surface waters and brings the nutrients up. Furthermore, the upwelling locations act as a source of kelp propagules for dispersing and recolonizing the locations without upwelling where the environmental conditions are suitable. The kelp abundance pattern was rather affected by the following water temperature drop during 1999–2000 (La Niña). The increase of sea urchin populations, especially *T. niger*, during La Niña period, added a significantly negative factor of overgrazing into the change of growth patterns and abundance of kelp (Vega et al., 2005). In contrast, in northern Chile, Peru, and California, where there were no upwelling events, the locations severely suffered the extinctions of *Lessonia* and *Macrocystis* populations during the same ENSO event (Fernández et al., 1999; Ladah et al., 1999; Lleellish et al., 2001; Edwards, 2004).

4 Conclusions and research gaps

This review shows the significance of the studies which have been conducted on the Chilean coast up to now and the potential for the future research. Despite the findings discussed in this paper, a few unanswered questions—research gaps—still remain:

(1) There is a great need to investigate the beach wrack of subtidal kelp species, which directly provide habitat for upper littoral zone organisms. It still remains unknown how the species-specific kelp biomass and retention time vary according to seasonality and latitude; what the biotic and abiotic factors impacting herein are; the species-specific associated organism assemblages (micro-, meio-, macro- and, even, megafauna) and dynamics along with the disintegrating algae tissue (Krumhansl and Scheibling, 2012). Duarte et al. (2010) conducted an extensive study which could serve as a great baseline for the future research hypothesis, to continue and amplify the research questions that include broader geographical scale (Duarte et al., 2010).

(2) A long-term environmental monitoring of kelp ecosystems capturing changes due to abiotic or anthropogenic impacts is lacking in Chile as well as throughout the world. The majority of kelp assessment studies were conducted in highly populated regions leaving out remote places such as the southern tip of South America, so there is a lack of a full image of subtidal kelp ecosystem dynamics and responses to human pressure (Friedlander et al., 2020). Wild kelp harvesting impacts on fish populations and nearshore assemblages, and their dynamics, should be addressed in future research efforts, including comparative studies from remote as well as anthropogenically impacted sites. Such data would also give useful tools for the evaluation of both direct and indirect goods and services associated with subtidal kelp habitats, and could help to improve the rocky subtidal marine habitat management strategies.

(3) Although the global predictions for kelp habitats are rather pessimistic (Krumhansl and Scheibling, 2012), yet considering the Chilean coast being greatly heterogeneous in terms of seascapes, habitat formations and temperature ranges, the changing climate might impose great variation in the resilience of subtidal forests along the extensive Chilean coastline (Vergés et al., 2014). Therefore, the site-specific data sets are needed for more accurate future projections of the persistence of kelp resources in Chile. Historical records of impacts and recovery dynamics after El Niño and La Niña events provide insights and base knowledge, which, if comprehensively understood, could facilitate the future projections for survival and distribution of kelp forest in a context of global ocean warming due to rapidly changing climate (McPhaden, 1999). Long-term collection of data on local scale could help to create accurate projections of

the chances of kelp forest survival along the extensive Chilean shoreline, depicting specific areas where the large-scale climatic events would have the strongest impact (Vega et al., 2005). The responses and resilience of natural ecosystems can be uneven within an ecoregion as the perturbation is very often caused by the abiotic factors coupled with a degree of local anthropogenic impacts that, combined synergistically, act as a far greater disturbance. There is a plethora of examples worldwide when habitats suffer long-term direct and/or indirect anthropogenic alterations, and thus, even the temporal changes in abiotic environment, such as a heatwave or a storm, lead into a habitat collapse without resources to recover (Crain et al., 2008; De Fouw et al., 2018; Arafeh-Dalmau et al., 2020). Therefore, the continuous long term research efforts taking into account the multiple factors and uneven anthropogenic disturbances should be prioritised both in Chile and worldwide (Smale and Wernberg, 2013).

(4) The kelp forests constituted by more than one kelp species facilitate greater species richness within the ecosystem, whereas a similar effect is exhibited by the monoculture kelp forest featuring dense understory of macroalgae (Pérez-Matus et al., 2007). Uncovering the triggers of physiological changes could help to understand the species' intraspecific relations within the kelp ecosystem.

These are the questions with great potential to be explored in future studies concerning ecosystem dynamics, connectivity and resilience potential, among others.

The kelp aquaculture potential in Chile is mainly concentrated for abalone feeding and alginate production, and the increasing demand for kelp products in the local and global markets may highly contribute to kelp overexploitation (Vásquez, 2008). The virtual disappearance of kelp locally not only vanishes the essential habitats for various marine fauna and flora, but also limits their resilience and dispersal (propagule flow) into neighbouring areas (Rothäusler et al., 2011b; Hermosillo-Núñez, 2020). Humankind was already using kelp goods and services along the Southeast Pacific coastline 10 000–15 000 years ago, even causing localised overexploitation. Nevertheless, due to migration constraints back in historical times, and relatively low human population, the kelp ecosystems could fully recover (Rick and Erlandson, 2008). Nowadays, Southeast Pacific kelp forests are vulnerable for both local and global pressures, such as top-down and bottom-up ecosystem control imbalance (removal of high trophic level and/or keystone species from kelp habitat), unsustainable wild kelp harvest, and a changing climate in addition to sporadic ENSO events. Nevertheless, new technologies and sustainable management strategies have a high potential to reduce at least the local pressures, such the unsustainable wild kelp harvesting (Vásquez, 2008; Vásquez et al., 2012; Correa et al., 2016). Together with publicly accessible knowledge and science communication that increases the kelp habitats' value in the general society, it could help to preserve the kelp forest ecosystem before irreversible damages occur.

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