Chapter 14
Cold-Temperate Seaweed Communities of the Southern Hemisphere

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Please note the Erratum to this chapter at the end of the book

14.1 The Regions and Their Basic Abiotic Conditions

In the southern hemisphere, two circumpolar fronts roughly define the boundaries of the cold-temperate region (Fig. 14.1). The southern limit, the Antarctic Polar Front (APF; also known as Antarctic Convergence), is characterized by cold (ranging 3–5°C) surface waters. The northern limit, the Subtropical Front (STF; also known as Subtropical Convergence), separates subtropical water in the north from sub-Antarctic water, and follows approximately the 10°C surface isotherm in winter and the 15°C surface isotherm in summer (Heath 1985; Parsons 1985; Lüning 1990; see also Chap. 3 by Eggert and Chap. 18 by Bartsch). The STF is a complex, irregular frontal zone with seasonal migration of up to 2° latitude (Nelson and Broom 2010). The large eastward-moving Antarctic Circumpolar Current (ACC; called also West Wind Drift) strongly determines the oceanography in the Southern Hemisphere (Orsi et al. 1995) (Fig. 14.1). The circulation of the ACC and circumpolar frontal zones strongly define the diversity, biogeography, and the ecology of seaweeds in all the adjacent coastal regions.

14.1.1 Southwestern South America Region

In the Southeastern Pacific coast of Chile, there are two major current systems, the southward Cape Horn Current and the northward Humboldt Current, derived from the ACC around 40°S (Fig. 14.1). In the south, the Cape Horn Current flows through the Drake Passage. Three major regions along the coast can be identified: the

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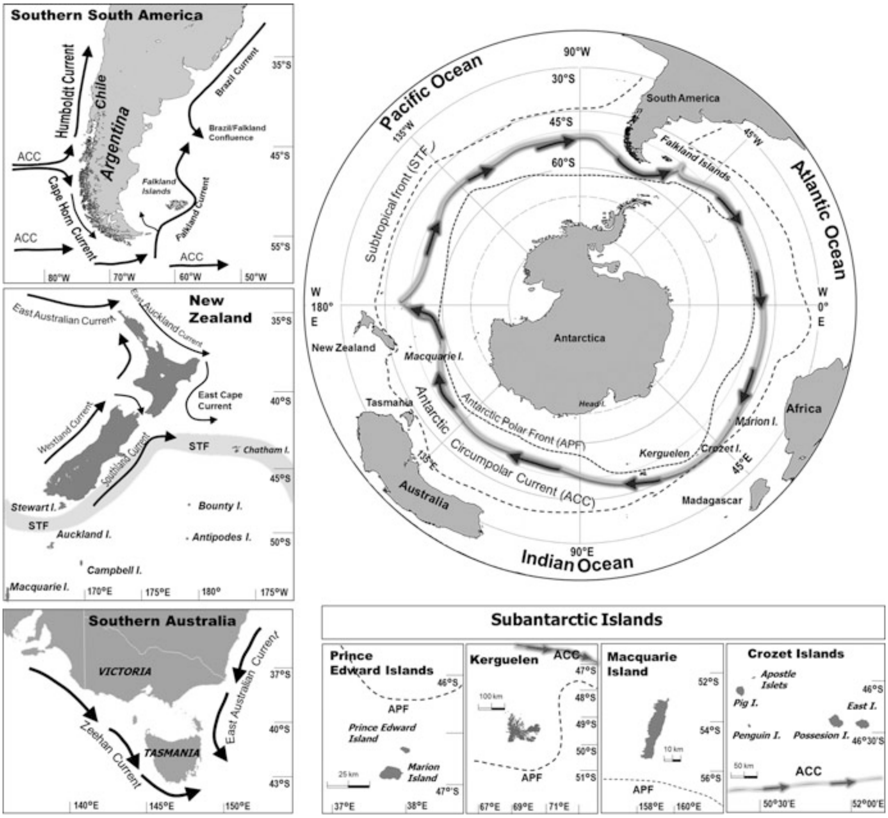

Fig. 14.1 The five cold-temperate regions of the southern hemisphere: southwestern South America, southeastern South America, Victoria-Tasmania, southern New Zealand, and the sub-Antarctic islands. Major oceanographic fronts, the Subtropical Front (STF; also known as Subtropical Convergence), the Antarctic Polar Front (APF; also known as Antarctic Convergence), and the Antarctic Circumpolar Current (ACC; called also West Wind Drift), are presented

southern Austral Fjords Region (sub-Antarctic, surface temperature 5–12°C), the Central/South Upwelling Region (Mediterranean characteristics, surface temperature 8–15°C), and the Northern Upwelling Region (subtropical, temperature 15–21°C) (Strub et al. 1998; Thiel et al. 2007; see also Chap. 18 by Bartsch). Habitats for seaweeds are characterized by exposed rocky shores between 18 and 41°S, while southwards the littoral systems exhibit higher variability with many fjords, archipelagos, and estuaries as well as glaciers (Santelices 1989).

14.1.2 Southeastern South America Region

In the coast of Argentina, the northward, cold-water (sub-Antarctic) Falkland current, derived from the ACC, meets the southward Brazil (subtropical) current around 36°S in an area called the Brazil/Falkland Confluence (Acha et al. 2004; Fig. 14.1). The cold-temperate section of the southeastern South America (approximately 41–55°S) is characterized by large bays and harbors, which provide heterogeneous habitats for seaweeds. Northwards of the Gulf San Matías (41°S), temperature increase and substrate become less suitable for seaweeds due to the massive runoff and sedimentation from Rio de la Plata (Acha et al. 2004). The Falkland Islands (Islas Malvinas), with sub-Antarctic characteristics, are situated in the path of the Falkland Current (Fig. 14.1) with water temperatures around 3–14°C (see also Chap. 18 by Bartsch). The coastal oceanography is characterized by the two branches of the Falkland Current, the weaker western branch (the Patagonian Current) rejoining the eastern branch north of the islands (Upton and Shaw 2002).

14.1.3 Victoria-Tasmania Region

The warm East Australian Current is the largest and the warm Leeuwin Current the second largest ocean current in Australia. The Leeuwin Current flows from the west Australian coast towards south-east, becoming the South Australia Current as it flows across the Great Australian Bight, reaching the west Tasmanian coast as the Zeehan Current (Fig. 14.1). The importance of these currents is evident from the tropical elements present in southern Australian waters at temperate latitudes. The southern coast of Tasmania is situated a few degrees north of the STF, the limit of sub-Antarctic waters (summarized by Poloczanska et al. 2007). However, in the coasts of Tasmania and Victoria, the surface water temperature remains cool, generally not exceeding 15°C in summer (Lüning 1990; see also Chap. 18 by Bartsch). The southern Australian coastline has large sections of rocky substrata, providing suitable habitats for seaweeds (Phillips 2001).

14.1.4 Southern New Zealand Region

Subtropical waters with relatively high salinity and temperature around New Zealand are mainly derived from the East Australian Current, while sub-Antarctic waters, with relatively low salinity and temperature, are driven north by the ACC. These two water masses meet in the STF (following roughly the 10°C winter and the 15°C summer surface isotherm; see also Chap. 18 by Bartsch). Along the east coast of the South Island, the Southland Current brings cool water towards north. It turns towards east and back to south around 40°S (Cape Turnagain), the northern limit for many species, combining with the warmer East Cape Current (Heath 1985; Parsons 1985) (Fig. 14.1). In the Fiordland region of the South Island, the exposed coastline is interrupted by channels, inlets, fjords, and many estuaries. Thus, the littoral systems in these locations are strongly influenced by the inflow of freshwater from rivers and glaciers (Nelson et al. 2002).

14.1.5 Sub-Antarctic Islands Region

The sub-Antarctic islands region consists of the island groups of Prince Edward (Prince Edward and Marion Islands), Crozet, Kerguélen, Heard (included also in the Antarctic region), and Macquarie (sometimes regarded in the Southern New Zealand region) Islands. The sub-Antarctic islands near New Zealand include Snares, Auckland, Campbell, Bounties, Antipodes, and Chatham Islands (Fig. 14.1). The location of the Southern Ocean islands in relation to the APF influences strongly their climatic conditions. Overall, these islands exhibit particularly cool, wet, and windy climates (Bergstrom and Chown 1999). The surface water temperatures along the coasts of the sub-Antarctic islands range 3–11°C in winter and 5–14°C in summer, depending on the geographical location (Lüning 1990).

14.2 Structure and Function of Seaweed Communities

14.2.1 Southwestern South America Region (Chile)

The southeastern Pacific coast can be divided into three biogeographic provinces: (1) the Peruvian province (from Peru to 30°S) with high presence of warm-temperate biota, (2) the Magellan province (from 40–42°S to 56°S) with dominance of sub-Antarctic cold-temperate elements, and (3) the intermediate area (from 30°S to 40–42°S) with mixed components from both provinces. According to Briggs (1974, cited in Lüning 1990) the cold-temperate region in the south-eastern Pacific is limited to the north at around 40°S (see also Chap. 18 by Bartsch et al.). Recent evidence (Strub et al. 1998; Camus 2001; Thiel et al. 2007) suggests that this region extends to around 30°S due to the influence of the Humboldt Current. In general, the seaweed flora in this region presents a remarkable degree of endemism (32%) (Santelices 1980), although recent accounts indicate increases in subtropical and alien species (Meneses and Santelices 2000; Castilla et al. 2005). Due to the higher occurrence of cold-temperate species, the total number of species increases southwards (Santelices 1980; Santelices and Marquet 1998). According to a recent update, the Magellan and Tierra del Fuego regions in the southern part of South America comprise 234 seaweed species (red 60%, brown 22%, green 18%) (Ramírez 2010). The species composition shows a break point around the latitude 42°S (Meneses and Santelices 2000).

In the wave-exposed coast at 30–55°S latitudes, the zonation and the structure of seaweed communities are characterized by the presence of *Porphyra columbina* and filamentous and foliose green algae such as *Ulva intestinalis* at upper littoral zones (Santelices 1989; Gómez and Huovinen 2011) (Fig. 14.2). In the mid-littoral, coarsely branched red algae such as *Mazzaella laminarioides and Nothogenia fastigiata* dominate. The red alga *Gelidium* sp. and the brown alga *Petalonia fascia*

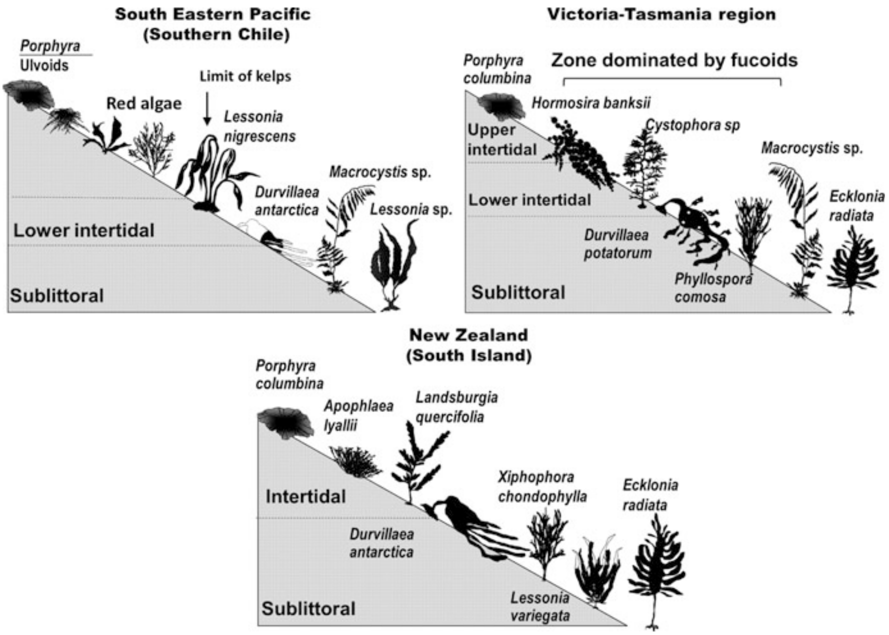

Fig. 14.2 General patterns of seaweed zonation, with dominant species in each littoral zone, in southern Chile, Victoria-Tasmania, and New Zealand (South Island) (the schemes represent a compilation of the literature revised in the text)

can colonize shaded pools and rocky crevices. The large kelp *Lessonia nigrescens* and the fucoid *Durvillaea antarctica* define the structure in the wave-battered infralittoral zone together with crustose/articulate species (*Corallina*) and red algae adapted to episodic erosion–accretion of sand such as *Ahnfeltiopsis durvillaei*. The sublittoral zone (up to 10 m) is characterized by a heterogeneous group with a dominance of kelps such as *Macrocystis pyrifera*, *Lessonia trabeculata*, *L. vadosa,* and *L. flavicans* (Villouta and Santelices 1986), mixed with thin leathery red algae (e.g., *Rhodymenia* sp. and *Callophyllis* sp.). Giant kelp forests are also found in protected bays and fjords, while the rhodophyte *Gracilaria chilensis* dominates in estuarine zones (Santelices 1980; Buschmann et al. 2004). At midlittoral and subtidal zones of the Magellan coast and some sub-Antarctic islands south of Tierra del Fuego (e.g., Diego Ramirez Islands), some species common to the Antarctic region (e.g., *Adenocystis utricularis*, *Iridaea cordata*, *Gigartina skottsbergii*, *Desmarestia* sp.) can be abundant (Santelices and Ojeda 1984; Westermeier and Rivera 1986).

The coexistence of *L. nigrescens* and *D. antarctica* at infralittoral zones conforms one of the most remarkable ecological associations. The spatial distribution and abundance of these two habitat-forming species result from complex interactions and morphofunctional adaptations, both species exhibiting different strategies to persist in areas with strong surf (Santelices et al. 1980; Westermeier et al. 1994). In general, factors determining the ecological functions of seaweeds have been well described for the ecosystems at 30–40°S (reviewed by Santelices 1989). At intertidal sites, trophic interactions with gastropods, such as the limpet *Fissurella*, the polyplacophoran *Chiton granossus,* and the snail *Tegula atra*, have important consequences for the seaweed communities (Moreno and Jaramillo 1983; Jara and Moreno 1984; Otaíza and Santelices 1985). At subtidal sites, the interaction between *M. pyrifera* and the sea urchins *Loxechinus albus* and *Tetrapygus niger* defines the ecological process of southern kelp forests (Santelices and Ojeda 1984; Dayton 1985). Unlike the situation for kelp forests of California, sea urchins from southern region preferentially consume algal drifts and act regulating the biomass of recruits (Moreno and Sutherland 1982; Vásquez et al. 1984; Graham et al. 2007). Some gastropods, such as *Tegula atra*, graze also on subtidal kelps (Moreno and Sutherland 1982; Buschmann 1992).

14.2.2 Southeastern South America Region (Argentinean Patagonia)

Approximately 400 seaweed species have been reported for the Atlantic coast of Argentina (reviewed by Lüning 1990). Two main biogeographical provinces have been proposed: (1) the Magellan province with cold water covering the southern Patagonia, and (2) the Argentinean province with warmer waters extending from North Patagonia (around Peninsula Valdés at 42–43°S) northwards (Lutz et al. 2003). In this region, species richness has been characterized as being relatively poor (Bolton 1994). Intertidal rocky shores here are characterized by a depauperate seaweed flora, mainly due to harsh physical conditions (Paruelo et al. 1998; Bertness et al. 2006), calcareous algae covering low tidal height in wave-protected sites (Bertness et al. 2006). Northwards from the Gulf San Matías (41°S), the massive runoff and sedimentation from Rio de la Plata limit the availability of hard substrates for seaweeds. In this region, temperate chlorophytes adapted to estuarine conditions dominate (Acha et al. 2004). Southwards, in the limit between the Argentinean and the Magellan biogeographical regions, subtropical species, such as *Dictyota*, are mixed with sub-Antarctic (e.g., *Bryopsis australis*) and endemic (e.g., *Myrogloia major*) components. The kelps *Macrocystis pyrifera*, *Lessonia flavicans,* and *L. vadosa* occur continuously from the Pacific to the Atlantic coast (up to 42°S for *Macrocystis*, 47–48°S for *Lessonia*) (Barrales and Lobban 1975; Searles 1978). The fucoid *Durvillaea antarctica* has its northern limit around 51°S in the Argentinean side of Tierra del Fuego (Boraso and Zaixso 2011). The invasive kelp *Undaria pinnatifida* has been associated with a decrease of species richness and diversity of native seaweeds in Patagonia (Casas et al. 2004; see also Chap. 12 by Andreakis and Schaffelke).

In the Falkland Islands, a total of 169 seaweed species (55% Rhodophyta, 29% Phaeophyceae, 16% Chlorophyta) were recently listed (Ramírez 2010). The lower intertidal zone is dominated by *Durvillaea antarctica*, while the subtidal zone is characterized by extensive *Macrocystis pyrifera* forests (van Tussenbroek 1993). Other large kelps, such as *Lessonia flavicans*, are also present (Ramírez 2010). Based on phylogenetic analyses, a highly diverse flora of bladed Bangiales (at least nine species) has been reported for the Falkland Islands (Broom et al. 2010). A high floristic similarity (60%) is found with the flora from Magellan-Tierra del Fuego region, principally due to species with a sub-Antarctic origin. The Falkland Islands and Magellan-Tierra del Fuego region form a group that separates from the Antarctic region (Hommersand et al. 2009; Ramírez 2010). These studies do not support the previously proposed biogeographic province with continuity of the marine flora in the Antarctic region and the sub-Antarctic South American region (John et al. 1994).

Ecological studies on seaweeds from the southeastern South American region are scarce, and thus the understanding of the distribution and abundance patterns as well as the functional roles of the seaweeds in these ecosystems is poorly known. Apparently, intertidal seaweed communities are strongly regulated by physical factors, as grazing pressure is weak due to the absence of common predaceous crabs and snails and the limited impact by limpets (Bertness et al. 2006). In subtidal environments, evidence based on population dynamics from Argentinean mainland and the Falkland Islands indicates that giant kelp beds are regulated by storms and nutrient availability (Barrales and Lobban 1975; van Tussenbroek 1989). In the kelp (*Macrocystis*) forests no consistent grazers, such as sea urchins, were reported either (Barrales and Lobban 1975). However, growth patterns and demography of these forests show considerable local variation (van Tussenbroek 1993).

14.2.3 Victoria-Tasmania Region

The seaweed flora of the southern Australia is characterized by high species richness and endemism (Bolton 1994; Phillips 2001; Kerswell 2006), resulting from a complex interaction of biogeographical, phylogenetic, and ecological processes (reviewed by Phillips 2001). Over 1,100 species (Bolton 1994) and four major floristic elements, i.e., endemic, widely distributed temperate, tropical, and polar elements, have been identified (Phillips 2001). Endemic (40–77%) and widely distributed temperate (17–45%) species account for the majority of the seaweeds, whereas species with tropical (4.5–9.7%) and polar (1.5–5.1%) affinities are much less represented. In Rhodophyta and Phaeophyceae, endemic elements dominate (77% and 59%, respectively), while in Chlorophyta widely distributed temperate (45%) flora account for the majority (Phillips 2001). Recent quantitative seaweed analyses confirmed the traditionally recognized Peronian (eastern), Flindersian (western), and Maugean (south-eastern) marine biogeographic provinces of the southern coast of Australia (Waters 2010). Furthermore, differentiation of marine communities in eastern and western elements has been associated with the Bassian Isthmus as a historical vicariant barrier (Waters 2008b; Fraser et al. 2009a).

The cold-temperate region of southern Australia (Victoria) and Tasmania is characterized by the dominance of fucoids, such as *Durvillaea potatorum* in the upper sublittoral zone in sites with high wave exposure (Cheshire and Hallam 1988) (Fig. 14.2). At medium-exposed sites the fucalean *Phyllosphora comosa* and the kelps *Macrocystis pyrifera* (former *M. angustifolia*) and *Ecklonia radiata* are common. In the intertidal zone, *Porphyra* dominate at higher locations, while at lower intertidal zones, the fucoid *Hormosira banksii* is abundant coexisting with green algae (e.g., *Codium*) and the Rhodophyta *Corallina*. Below the fringe of *H. banksii*, in the eulittoral zone *Cystophora torulosa* is the dominant fucoid. In southern Tasmania, *M. pyrifera* can form dense sublittoral forests in some locations, the upper sublittoral zone being dominated by *D. potatorum* and the endemic *Lessonia corrugata*. In general, many of the dominant fucoids are restricted to cold-temperate waters, and only *P. comosa* and *H. banksii* have distribution along the warm-temperate eastern coast of Australia (to a latitude 32°S). The northern limit of *D. potatorum* is at latitude 36°S, *M. pyrifera* (former *M. angustifolia*) extending to the northern border of Victoria (Lüning 1990).

Large brown algae, due to their size and foundational character, have been a special topic in many ecological studies (Sanderson and Thomas 1987). In the east coast of Tasmania, the sea urchins *Heliocidaris erythrogramma* and *Centrostephanus rodgersii* and the abalone *Haliotis rubra* regulate the population dynamics of various canopy-forming algae such as *Phyllospora comosa* and *Ecklonia radiata* (Valentine and Johnson 2005; Ling and Johnson 2009). Interestingly, the sea urchin barren zone is rapidly colonized by the introduced kelp *Undaria pinnatifida* (Valentine and Johnson 2004, 2005). In Tasmania, overgrazing of seaweeds by introduced sea urchin *Centrostephanus rodgersii* together with oceanographic changes is causing dramatic decline in the giant kelp beds (Johnson et al. 2011).

14.2.4 Southern New Zealand Region

Coasts of New Zealand represent areas of high seaweed diversity (Norton et al. 1996; Kerswell 2006). A recent account indicated that of the 770 currently known seaweed species, 265 are endemic (34%) and 22 alien (2.9%) (Hurd et al. 2004). According to the revision of Parsons (1985), the South Island hosts around 497 species, while for the North Island 555 species were reported. Rhodophyta accounts for around 60% of the total taxa, Chlorophyta and Phaeophyceae each contributing with approximately 20% (Parsons 1985). Within the cold-temperate southern New Zealand region are included the South Island, the southern part of the North Island, and the Stewart Island. Also the sub-Antarctic islands Auckland, Campbell, Antipodes, and Bounty, as well as the Chatham Island, are in this region (Fig. 14.2).

Although lower in number compared to green and red algae, brown algae, particularly fucoids, dominate the rocky shores of Southern New Zealand, while only few kelps can be regarded as dominant organisms (Schiel 1990) (Fig. 14.2). In the middle and lower intertidal zone, *Cystophora torulosa* and *Landsburgia* *quercifolia* are abundant, while *Durvillaea antarctica* is the most conspicuous brown alga in the lower littoral fringe at exposed sites, accompanied by red algae such as *Gigartina*, *Laurencia*, *Polysiphonia*, *Caulacanthus*, *Gelidium,* and *Nemalion*, the brown algae such as *Hormosira banksii* and *Colpomenia sinusosa*, and the green algae *Codium* and *Caulerpa*. In the southern part of the North Island (Wellington), the fucalean species *L. quercifolia*, *Carpophyllum flexuosum*, *C. maschalocarpum,* and *C. angustifolium* and the laminarian *Lessonia variegata* are common in shallow waters. *Macrocystis pyrifera* and *Ecklonia radiata* generally reach their highest abundance in deeper waters (Schiel 1990).

In Fiordland in the South Island, the lower intertidal is dominated by *Durvillaea antarctica,* particularly in the east coast. At around a depth of 2 m, the fucalean species *Xiphophora chondrophylla* is abundant. *Ecklonia radiata* is common at 3–6 m and at 12–18 m depth zones (Schiel 1990; Villouta et al. 2001). The upper sublittoral zone is inhabited by *Lessonia variegata* as well as *D. willana*, which is endemic to New Zealand (Cheshire et al. 1995). In sheltered rocky shores within the fjords, diversity and structure of seaweed assemblages have been less studied. Surveys carried out in Doubtful Sound (45°S) indicated the presence of, e.g., red alga *Pachymenia lusoria* and diverse *Ulva* species in the most estuarine locations. The lower intertidal zones are characterized by *D. antarctica*, *Xiphophora chondrophylla,* and sparse populations of *M. pyrifera* (Boyle et al. 2001).

The structure and function of seaweed communities from the New Zealand cold-temperate region, especially of fucalean and kelps, have been well addressed in some locations. However, many aspects of population dynamics and underlying processes such as phenology, dispersal, and recruitment have not been intensively addressed (reviewed by Hurd et al. 2004; Schiel 1990, 2004). On the other hand, biotic control of seaweed assemblages is different between regions from the main islands, which reflect their intrinsic differences in seaweed structure and composition (Schiel and Hickford 2001). For example, the impact of the sea urchin *Evechinus chloroticus* on different large brown algae is higher in northern communities dominated by *Ecklonia*, compared to communities dominated by cold-temperate seaweeds, e.g., in Fiordland and Chatham Island, where the *Ecklonia* stands are replaced by fucoids and other kelps such as *Lessonia* spp. (Schiel 1990; Villouta et al. 2001). The presence of large brown algae has different impact on understory species, especially red algae (Lilley and Schiel 2006), and in systems where the control by herbivores is less intense, the interspecific competence between large canopy-forming seaweeds can become a relevant factor (Schiel and Hickford 2001).

14.2.5 Sub-Antarctic Islands Region

According to a catalog of Papenfuss (1964), the seaweed flora of the sub-Antarctic islands and the Antarctic region contains 550 species, approximately half being endemic to these two regions, while approximately 75% of these species are distributed in the sub-Antarctic islands (Clayton 1994). These regions share a considerable number of cold-temperate species, e.g., the brown alga *Adenocystis utricularis*, the red alga *Iridaea cordata* and *Gigartina skottsbergii*, however, some endemic Antarctic species such as *Himantothallus grandifolius* and *Ascoseira mirabilis* do not inhabit the sub-Antarctic islands (Lüning 1990; Clayton 1994). The distribution of the endemic Antarctic rhodophyte *Palmaria decipiens* just extends to Macquarie Island (Wiencke and Clayton 2002). On the other hand, the circumpolar kelps *Macrocystis pyrifera* and *Lessonia* spp. as well as the large intertidal fucoid *Durvillaea antarctica* are absent from the Antarctic (John et al. 1994; Clayton et al. 1997).

The general zonation pattern for the shores of Macquarie Island has been described to comprise an upper littoral *Porphyra* zone, a "bare" zone (dominated by siphonariid mollusc *Kerguelenella lateralis*), an upper red algal zone (*Rhodymenia* sp., *Chaetangium fastigiatum*, *Palmaria georgica*, *Acrosiphonia pacifica*, *Porphyra columbina*), a kelp zone (*Durvillaea antarctica*), and lower red algal zone below the infralittoral with understory species such as *Delesseria* spp., *Iridaea* sp., and *Desmarestia* sp. (Kenny and Haysom 1962; Smith and Simpson 2002). Similarly, in Marion Island, *D. antarctica* is the dominant species at the infralittoral fringe, while *Desmarestia rossii* and *Durvillaea* sp. occur in a zone of 3–6 m. Encrusting coralline algae are particularly abundant in shallow areas (Beckley and Branch 1992). At subtidal locations, beds of the endemic *Macrocystis laevis* are abundant (Perissinotto and McQuaid 1992; Beckley and Branch 1992). In general, infralittoral *D. antarctica*, shallow-water encrusting coralline algae, *Desmarestia* spp., and subtidal *Macrocystis* beds seem to overall characterize the benthic seaweed communities in many sub-Antarctic islands (Beckley and Branch 1992).

For the sub-Antarctic islands near New Zealand, 14–148 seaweed species have been reported, with the highest species richness being recorded for Chatham Islands and the lowest for the Bounty Island (Parsons 1985). Although notable differences in species composition and dominance patterns can exist among islands (Freeman et al. 2011), *Durvillaea antarctica* and *Macrocystis pyrifera* occur in all these island groups, *Lessonia flavicans* reported for Auckland, Campbell, the Antipodes, and Bounty. The fucalean *Xiphophora chondrophylla* is present in all the island groups, except for the Bounty (Lüning 1990). Endemic *Durvillaea* species have been proposed for the Antipodes (undescribed species) and Chatham Island (*D. chathamensis*) (Cheshire et al. 1995; Fraser et al. 2010b; Fig. 14.3). In the light of a re-examination of the description of *Porphyra columbina* using molecular techniques, this species is distributed in the Auckland, Campbell, Antipodes, Chatham, and Falkland Islands, with a very restricted distribution in mainland New Zealand (Nelson and Broom 2010).

In the Chatham Island, the shallowest subtidal areas are dominated by *Durvillaea*. Several fucalean species (e.g., *Xiphophora chondrophylla*, *Carpophyllum plumosum* and *C. maschalocarpum*) are abundant to a depth of around 10 m, *C. flexuosum* occurring mostly in deeper waters (9–20 m). The endemic *Lessonia tholiformis* and *L. variegata* are abundant at 2.5–15 m depth. In some sites, *Macrocystis pyrifera* forms dense beds at 15–20 m depth. In the Auckland Islands,

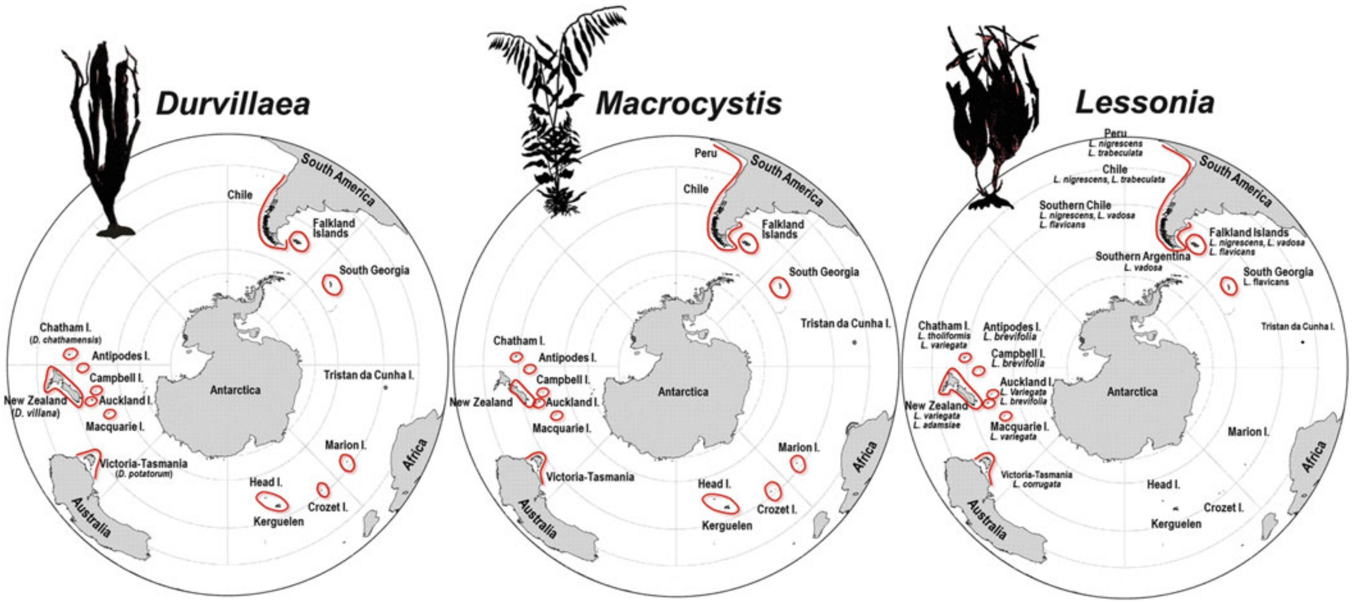

Fig. 14.3 Distribution of the large brown algal genera *Durvillaea* and laminariales *Macrocystis* and *Lessonia* in the southern hemisphere. Different species of *Durvillaea* and *Lessonia* are presented. As the current evidence indicates the existence of only one species of *Macrocystis* (*M. pyrifera*) (see the text), this information is presented as *Macrocystis* sp. Note: *Macrocystis* is also present in the northern hemisphere in the Pacific coast from Baja California, Mexico, to Alaska (the schemes represent a compilation of the literature revised in the text)

shallowest areas are also dominated by *D. antarctica*. *Xiphophora* is common at 2 m depth and *Halopteris funicularis* around 2–5 m. *Lessonia brevifolia* forms beds around 4–12 m depth, *M. pyrifera* being abundant in deep waters. The laminarian *Ecklonia radiata,* the most common kelp of New Zealand, has not been recorded neither at the Chatham nor the Auckland Islands (Schiel 1990; Schiel et al. 1995).

The ecology of the seaweed communities from the sub-Antarctic islands region is poorly known. The harsh environmental conditions as well as the remoteness and inaccessibility of many islands impede experimental studies. The scarce studies characterizing the structure and functions of seaweeds of intertidal zones reveal that physical environmental factors exert a strong control on these assemblages, probably regulating also the action by herbivores (Smith and Simpson 2002; Freeman et al. 2011). On the other hand, the importance of the habitat-forming species *Durvillaea antarctica* on the ecology of the littoral system has been emphasized (Klemm and Hallam 1988; Smith and Simpson 2002). In subtidal areas of these islands, the biological processes occurring within the *Macrocystis* forests have been also studied (Dayton 1985; Graham et al. 2007), including aspects related with their trophic role in the food web (Kaehler et al. 2006), aspects of primary production, and geochemical cycles (Delille et al. 2009).

14.3 Biogeographical Processes

The development of the ACC as a result of the opening of the Tasmanian Gateway between Australia and Antarctica (~33 Ma) and the Drake Passage between South America and Antarctica (~23 Ma) permitted the circumpolar distribution of biota in the southern hemisphere (Clayton 1994). Many cool water taxa evolved in the early Tertiary at high latitudes (the so-called Weddellian species) and colonized lower latitudes, e.g., Tierra del Fuego in southern South America (Lüning 1990). A relatively recent long-range dispersal across the Southern Ocean is reflected in many species reported in South America, the Falkland Islands, and various sub-Antarctic islands (Clayton 1994; see also Chap. 17 by Rothäusler et al.).

In order to interpret the present distribution patterns and origin of biota in the southern hemisphere, different theories dealing with separation through plate tectonics, long-distance dispersal during different periods, and the role of the formation of the ACC linking the land masses have been proposed over the last decades. Models of the species distribution involving ACC dispersal were widely replaced by vicariance and the role of past geological events (plate tectonic) (Cheshire et al. 1995; Waters 2008a). However, recent evidence based on new molecular techniques emphasizes the role of dispersal in distribution of marine biota in the southern hemisphere and relates some evidence of vicariance in southern waters with more localized and recent vicariant models, e.g., the isolation by the Bassian Isthmus that connected Tasmania with Australia during Pleistocene low sea-level, rather than with plate tectonics (Waters 2008a; Fraser et al. 2009a). Recent ecological, phylogenetic, and phylogeographic studies suggest also that rafting cannot be ignored as an important mechanism of long-distance dispersal in southern waters (Waters 2008a; see also Chap. 17 by Rothäusler et al.).

14.3.1 Cold-Temperate Kelps as Biogeographical Models

The large “bull kelp” *Durvillaea* has proved to be an interesting model for seaweed biogeography. This genus has five recognized species: one (*D. antarctica*) is buoyant and with circumpolar distribution, while other four are nonbuoyant and with restricted distribution (*D. willana* present in southern New Zealand, *D. potatorum* in southern Australia and Tasmania, *D. chathamensis* in Chatham Islands, an undescribed species *Durvillaea* sp. in Antipodes Islands) (Cheshire et al. 1995) (Fig. 14.3). Recently, a phylogeographic circum-sub-Antarctic study provided evidence of recent (postglacial) recolonization by *D. antarctica*, most probably by transoceanic rafting of adult specimens (see also Chap. 17 by Rothäusler et al.). This is supported by high genetic homogeneity over vast geographic distances in sub-Antarctic latitudes, while along the coasts of New Zealand and Chile, substantial genetic differentiation was detected over relatively small geographic distances (e.g., tens of kilometers) (Fraser et al. 2009b).

In the coast of Chile, two different lineages of *D. antarctica* with a biogeographic break at 44–49°S have recently been revealed. Interestingly, populations from southern Patagonia (49–56°S) were found to be genetically homogenous and identical to a haplotype found throughout the sub-Antarctic region, pointing to the transoceanic ancestry and a relative recent recolonization (since the Last Glacial Maximum) (Fraser et al. 2010a). Similarly, genetically distinct species have been postulated for two populations of *D. antarctica* in New Zealand (Fraser et al. 2009c). Under a phylogenetic species concept, the genus *Durvillaea* has been recently interpreted as a complex of nine distinct evolutionary lineages, only one of which has an intercontinental distribution (Fraser et al. 2010b).

The most widely distributed kelp, *Macrocystis* (Fig. 14.3), displays an amphi-equatorial distribution. Four species (*M. pyrifera*, *M., integrifolia*, *M. angustifolia,* and *M. laevis*) are currently recognized, however, increasing evidence strongly suggests the existence of a single morphologically plastic species (reviewed by Graham et al. 2007; Demes et al. 2009). Phylogenetic analyses by Coyer et al. (2001) point to a very recent (0.01–3 Ma) dispersal of *Macrocystis* from the northern to the southern hemisphere. This direction of the dispersal was supported by the greater genetic diversity of the individuals of the northern hemisphere, displaying paraphyletic clades, while the southern individuals formed monophyletic clades and showed little genetic differentiation across a wide southern geographic range, which refers to a recent dispersal.

Unlike the floating *D. antarctica*, the species of the genus *Lessonia* show a disperse distribution along the southern hemisphere (Fig. 14.3) characterized by a remarkable regional endemism (Searles 1978). The only intertidal species, *L. nigrescens*, extends from 17°S to 56°S and is the dominant organism at the infralittoral zone of the wave exposed locations of Chile and Peru (Santelices 1989). The subtidal *L. trabeculata* has a distribution range from 12 to 41°S in the eastern Pacific coast (from Peru to Chiloé Island) (Villouta and Santelices 1986). Populations of *L. vadosa* are found in the southern South America (47–56°S) in the coasts of Chile and Argentina as well as in the Falkland Islands (Searles 1978; Scrosati 1991). *L. flavicans* has also been described for South Georgia (John et al. 1994). *L. variegata* is endemic to New Zealand region including the mainland (Schwarz et al. 2006) and some adjacent islands (Chatham, Auckland, and Macquarie) (Kenny and Haysom 1962; Hay 1981). Other species show restricted distribution in this region, *L. tholiformis* being *e*ndemic to Chatham Island (Hay 1989), *L. brevifolia* present in Auckland, Campbell, Antipodes, and Bounty Islands (Hay 1981, 1987), *L. adamsiae* in Snares Islands (Hay 1987), and *L. corrugata* in Tasmania (Lane et al. 2006) (Fig. 14.3).

Recent phylogeographic analyses indicated the presence of two main divergent lineages, possibly two cryptic species, within *L. nigrescens* of the coast of Chile (Tellier et al. 2009), which matches the biogeographical transition zone around 30°S. In this species complex, a very limited dispersal has been reported (Faugeron et al. 2005; Tellier et al. 2009), confirming the marked endemism in many regions. Apparently, environmental factors (e.g., temperature) and anthropogenic activities can reduce gene flow between populations of *L. nigrescens* (Faugeron et al. 2005; Oppliger et al. 2011). Despite some molecular analyses (Lane et al. 2006), the origin of the genus *Lessonia* still remains unclear. Interestingly, within Lessoniaceae, it is the only genus not present in the northern hemisphere, and furthermore, it does not appear to be closely related to the other genera of this family (Bolton 2010).

14.4 Major Differences with Cold Temperate Regions of the Northern Hemisphere

Cold-adapted seaweeds are believed to have developed during the Tertiary decline of seawater temperature in temperate and polar regions. A permanent separation of the southern and northern hemisphere cold-water flora was produced by the formation of the pan-tropical Tethys Sea during the Mezozoic era (251–65 Ma). The presence of amphi-equatorial species with cold-temperate characteristics might be the result of processes such as paleoclimatic vicariance during the Miocene when intrusion of glacial water masses allowed many species crossing the equator (Lüning 1990; see also Chap. 18 by Bartsch et al.). However, some evidence indicates that disjunctions for some species are of a recent origin, e.g., during the last Pleistocene glacial maximum (18,000 years ago) (van Oppen et al. 1994). In the genus *Macrocystis*, phylogenetic analyses point to a very recent (0.01–3 Ma) dispersal from the northern to the southern hemisphere (Coyer et al. 2001). These transequatorial migrations took place at the east side of the oceans where the tropical regions are compressed. Crossing the equator was facilitated by "stepping stones," as well as by further constriction of the tropical regions during the Pleistocene and by glacial temperature drops as high as 8°C (reviewed by Lüning 1990; see also Chap. 18 by Bartsch et al.).

Compared to the cold-temperate regions in the northern hemisphere, the southern hemisphere has been characterized by the greater importance of the prevailing ocean currents for the seaweed distribution as well as by a more pronounced geographical isolation of the seaweed flora (Lüning 1990). In the southern hemisphere, the cold temperate regions have more island-like or peninsular character, thus resulting in a higher endemism. In the northern hemisphere, migrations at higher latitudes are possible mainly along coastlines. Since its formation the ACC has been the dominating biogeographical element at cold-temperate latitudes of the southern hemisphere and has served as a migration route for floating seaweed species (e.g., *Macrocystis pyrifera* and *Durvillaea antarctica*) creating similarities in floras between these regions (Lüning 1990; Fraser et al. 2009a; see also Chap. 17 by Rothäusler et al.).

One of the striking differences between the northern and southern cold-temperate regions is the almost exclusive dominance of species of the order Laminariales in littoral systems in the northern hemisphere, whereas in the southern hemisphere the only genera of the Laminariales, i.e., *Macrocystis*, *Lessonia*, *Ecklonia*, *Eisenia,* and *Laminaria*, grow intermixed with various dominant fucalean species. Nearshore reef assemblages in temperate New Zealand and Australia differ from those in other parts of the world: fucalean seaweeds dominate in the shallow subtidal zone, the kelp *E. radiata* forms dense beds at middle depths, and the giant kelp *M. pyrifera* occurs in the southern regions, but is abundant at only a few sites (Schiel et al. 1995). In the mid-intertidal zone, *Chondrus crispus*, a common dominant rhodophyte in the northern hemisphere, is replaced in regions of southern South America and many sub-Antarctic islands by species of *Nothogenia* and by the brown alga *Adenocystis utricularis* (Westermeier and Rivera 1986; Ingólfsson 2005). Among the main similarities between the northern and southern hemisphere cold-temperate floras is the presence of various members of the order Desmarestiales. In the coast of southern Chile, South Africa, and many sub-Antarctic islands several species of *Desmarestia* are regional endemics, and some species such as *D. ligulata* and *D. confervoides*/*D. viridis* exhibit a disjunct amphi-equatorial distribution (Wiencke et al. 1994; Peters et al. 1997). Species such as *D. anceps*, *D. menziesii,* and *Himantothallus grandifolius* are dominant in the Antarctic, but absent from the cold-temperate region. These species are regarded as ecological equivalent of Laminariales in the northern hemisphere (Moe and Silva 1977; Clayton 1994; Wiencke et al. 1996).

14.5 Concluding Remarks

Seaweed flora in the cold-temperate regions of the southern hemisphere has been modified not only by large-scale geological and paleoclimatic processes but also by long-distance dispersal events and an inherent capacity of the species to adapt to new habitats. Diverse present and future threats arising from anthropogenic activities will impose new challenges for these seaweeds communities. Many related aspects, such as temperature rise (see also Chap. 18 by Bartsch et al.), ocean acidification (see also Chap. 19 by Roleda and Hurd.), stratospheric ozone depletion and solar UV-B radiation (see also Chap. 20 by Bischof and Steinhoff), marine eutrophication and pollution (see also Chap. 21 by Teichberg.), as well as invasive seaweed species (see also Chap. 12 by Andreakis and Schaffelke.) and aquaculture (see also Chap. 22 by Buchholz et al.), are addressed in more detail in separate chapters throughout this book.

One of the most important issues is the scarce basic knowledge on the seaweeds communities over large areas. Although advances have been made in some regions, such as central/southern Chile, southern Australia, and New Zealand, seaweed communities of, e.g., the fjord region of southern Chile, the Argentinean region, and many sub-Antarctic islands are poorly known, partly due to their remoteness. The lack of studies on species diversity, community structure, and function of seaweeds in these locations impede suitable estimations on their contribution to the global geochemical fluxes, the potential genetic loss due to environmental shifts, and, in general, their conservation status. These are basic elements to understand the potential for tolerance and resilience in scenarios of global change (Harley et al. 2006).

Due to the closeness of the Antarctic ozone hole, the increase of solar UV-B radiation and resulting adverse effects on the biota of the cold-temperate region in the southern hemisphere is of a concern. Considering the latitudinal gradients of UV radiation and episodes of stratospheric ozone depletion reaching latitudes as low as 40°S (Orce and Helblin 1997), it is reasonable to argue that this factor can impose geographical barriers to species exhibiting low stress tolerance capacity. Recently, the potential effects of enhanced ultraviolet radiation on seaweed physiology have been examined in the context of adaptations to the intertidal life both in the Pacific and Atlantic coasts of Patagonia (Häder et al. 2003; Gómez et al. 2004; Huovinen et al. 2006; Rautenberger et al. 2009; Huovinen and Gómez 2011).

In some islands of the Southern Ocean, especially in Marion, Kerguelen, and Macquarie Island, a marked climate change, expressed as increases in temperature and declines of precipitation, has begun to be examined in the context of global warming. Because of the closeness of these islands to the APF, a relatively mobile climatic boundary, the impact of these climate shifts and its relation with, e.g., invasion of species in these islands has drawn attention, hitherto for terrestrial ecosystems (Bergstrom and Chown 1999). In Tasmania, intensification of southward intrusions of warmer, nutrient-poor East Australian Current waters has been reported to cause ocean warming and transport of biota to eastern Tasmania. The shift in large-scale oceanography has been related with a decline in the extent of the giant kelp beds. Furthermore, overgrazing of seaweeds by a recently established sea urchin species is affecting fundamentally the rocky reef systems in Tasmania (Johnson et al. 2011).

As seaweed communities of the cold-temperate region in the southern hemisphere are relatively isolated and thus, their structure, function, and biogeographic processes are strongly dependent on the environmental context, the direct impact of human activities requires urgent attention. Important questions related with impact of fish aquaculture and industrial effluents, introduction of alien species, and the overexploitation of commercially important seaweeds have not been addressed in detail. This information clearly is essential in order to understand the ecological processes of these organisms and their adaptive potential to large-scale physical forcings.

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