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CONCISE REVIEWS: SEAWEEDS OF COMMERCIAL INTEREST

Concise review of the genus *Durvillaea* Bory de Saint-Vincent, 1825

Marcel Velásquez[1,2,3] · **Ceridwen I. Fraser**[4,5] · **Wendy A. Nelson**[6,7] · **Fadia Tala**[8,9] · **Erasmo C. Macaya**[10,11]

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Abstract

The genus *Durvillaea* includes six currently accepted species, as well as two newly proposed species. *Durvillaea* spp. have a diplontic life cycle, lack a free-living gametophyte and have oogamous reproduction. All *Durvillaea* species require rocky substrate for attachment and wave-exposed environments. These "southern bull kelps" occur exclusively in the Southern Hemisphere and are important foundation species, in most cases controlling local community structure, influencing biodiversity, and providing food and habitat for other culturally and economically important species. Most species are non-buoyant and these have restricted geographic ranges, in some cases endemic to small oceanic islands. Buoyant members of the genus are more widespread, with one species (*Durvillaea antarctica*) found throughout the subantarctic, Chile, and New Zealand. This chapter summarizes the taxonomy, biology, and economic importance of *Durvillaea* species, with a focus on aspects relevant to their availability and productivity as crop plants. Systematics, distribution, ecology, life histories, population status, harvesting times, protection, management and chemical composition are covered. Much of the available data are for the species *Durvillaea antarctica*, *D. willana*, and *D. potatorum*. The techniques used in harvesting and the human uses of *Durvillaea* spp. (e.g., as food) are described, along with recommendations for harvest timing and methods.

Keywords *Durvillaea* · Biology · Harvest · Population status · Economic importance

Identity: genus and species

The genus *Durvillaea* was described by Bory de Saint-Vincent in 1825. The type species of the genus is *Durvillaea utilis* Bory 1825: 22 [594], nom. illeg., with the type locality: Îles Malouines [Falkland Islands] (in Dumont d'Urville 1825: 22). The name *Durvillaea utilis* was illegitimate as it was a later synonym of *Fucus antarcticus* Cham. (described in Choris 1822: 7, pl. 7). Hay (1979a) notes that "The figure used by Bory to illustrate *D. utilis* (PI. 5) is a copy of Chamisso's original illustration of *Fucus antarcticus*." The combination *Durvillaea antarctica* (Cham.) Har. was made by Hariot in 1892.

✉ Marcel Velásquez
marcelvelasquez2@gmail.com

[1] Laboratorio de Ecosistemas Marinos Antárticos y Subantárticos (LEMAS), Universidad de Magallanes, Punta Arenas, Chile

[2] Institute of Ecology and Biodiversity (IEB), Las Palmeras 3425, 8320000 Santiago, Ñuñoa, Chile

[3] Institut de Systématique, Évolution, Biodiversité (ISYEB, UMR7205 CNRS, MNHN, UPMC, EPHE), Muséum national d'Histoire naturelle, Sorbonne Universités, 57 rue Cuvier, 75005 Paris, France

[4] Fenner School of Environment and Society, Australian National University, Building 46 Cunningham Close, Acton, ACT 2601, Australia

[5] Department of Marine Science, University of Otago, PO Box 56, Dunedin 9054, New Zealand

[6] National Institute of Water and Atmospheric Research Ltd. (NIWA), Private Bag 14901, Wellington 6241, New Zealand

[7] School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

[8] Departamento de Biología Marina, Universidad Católica del Norte, Larrondo, 1281 Coquimbo, Chile

[9] Centro de Investigación y Desarrollo Tecnológico en Algas (CIDTA), Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo, 1281 Coquimbo, Chile

[10] Departamento de Oceanografía, Universidad de Concepción, Concepción, Chile

[11] Centro FONDAP de Investigaciones en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Valdivia, Chile

Although Kūtzing (1843) described the genus *Sarcophycus*, with the type species *Sarcophycus potatorum* (Labill.) Kütz., Areschoug (1854) transferred this species to *Durvillaea*, recognizing *Sarcophycus* to be a heterotypic synonym.

There are 6 species of *Durvillaea* that are currently accepted:

Durvillaea potatorum (Labill.) Aresch. 1854
Durvillaea antarctica (Cham.) Har. 1892
Durvillaea willana Lindauer 1949
Durvillaea chathamensis C.H.Hay 1979
Durvillaea poha C.I.Fraser, H.G.Spencer & J.M.Waters 2012
Durvillaea amatheiae X.A.Weber, G.J.Edgar, S.C.Banks, J.M.Waters & C.I.Fraser 2017

As *D. poha* and *D. amatheiae* have only recently been recognized, split from *D. antarctica* and *D. potatorum* respectively, earlier research on *D. antarctica* and *D. potatorum* could include these unrecognized species. In this chapter, references to our knowledge of *D. antarctica* prior to 2012, and *D. potatorum* prior to 2017, should be considered to potentially include or refer to the newly described species.

In addition, recent research (under review) recognizes another two species, one from the Antipodes Islands, in the New Zealand subantarctic, and one from central Chile.

There are two species; one placed in *Durvillaea* that is now considered to belong to other genera: *Durvillaea simplex* Suhr—described from Sptizbergen is probably a laminarian (Hay 1979a), and *Durvillaea porra* (Léman) Gaillon—described from the Northern Hemisphere (California) and currently placed in the laminarian genus *Pelagophycus.*

Genus *Durvillaea* Bory

Massive thallus to 10-m long, with a large discoid holdfast, a robust stipe, and leathery fronds divided from near the base or from above into stipitate, ligulate, or broad blades. Growth is diffuse in the upper part of the blades. Thallus structure is essentially haplostichous and differentiated into a meristoderm with relatively small cells arranged in radiating files and containing numerous physodes and chloroplasts, grading into a cortex of larger vacuolate cells and medulla of intertwined hyphal filaments with or without air chambers. Extensive deposits of intercellular wall material are present. Discoid chloroplasts lack pyrenoids.

Durvillaea amatheiae X.A.Weber, G.J.Edgar, S.C.Banks, J.M.Waters & C.I.Fraser 2017: 637, Fig. 2b

This species has the following characteristics: rarely exceeding total lengths of 5 m, with thalli generally dark brown to dark tan proximally, becoming lighter distally. Individuals anchored by a thick, crustose non-perforate holdfast, not found to support burrowing invertebrates. Stipe to at least 50 cm in length, typically wider in diameter at the bottom than the top. Stipes fan distally through an apophysis into a laminar blade, with sections 5–30-cm wide and to at least 450-cm long. Up to 40 distichous, lanceolate to falcate marginal proliferations (stipitate lateral blades), highly variable in length from 50 mm to lengths exceeding primary blade length. Palmate region infrequently divided into distinct rounded boughs “branches” (sensu Hay 1977). Thalli with no internal honeycomb structure (“solid” bladed).

Durvillaea antarctica (Cham.) Har. 1892: 1432

Basionym: *Fucus antarcticus* Cham. in Choris 1822: 7, pl. 7

Synonyms**:**
Durvillaea utilis Bory 1825
Halymenia incurvata Suhr 1839
Laminaria caepaestipes Mont. 1839
Durvillaea mastix Suhr 1841
Ecklonia caepaestipes (Mont.) Endl. 1843
Durvillaea harveyi Hook.f. 1845
Durvillaea montagnei Kütz. 1849
Durvillaea caepaestipes (Mont.) Skottsb. 1919

Common names:

Chile: Huilte, ulte, lunfo, coyofe, kollof, collofe (words from Chilean indigenous population, “Mapudungun” language), cochayuyo, cochahuasca and raguay.

New Zealand: Rimurapa (Māori)

Australia and New Zealand: bull kelp or southern bull kelp.

Thalli are massive with the leathery blades divided into strap-like branches, 3–5 (10)-m long, extending from the cylindrical trunk-like stipe, and dome-shaped holdfasts that are usually excavated by burrowing invertebrates. It has blades with an internal honeycomb structure giving buoyancy to the thalli. The shape and width/length as well as the splitting of the blade into long straps or thongs are influenced by the wave exposure of the sites where this species is found. In more exposed areas, blades become narrower and more whip-like; however, they always remain rounded or oval in cross-section. Its color is golden to dark brown to olive green. Fertile structures are scattered over the blades but are not easily visible. *Durvillaea antarctica* is present in the low intertidal zone on wave-exposed coasts.

Durvillaea chathamensis C.H.Hay 1979a: 196, Figs. 2, 6–8

Thalli grow up to 15-m long and are made up of massive blades, usually not divided, flattened with parallel sides and wavy edges, and with no internal honeycomb structure (“solid” bladed). Stipe is unbranched and grows from a large, dome-shaped holdfast that is usually excavated by burrowing invertebrates. Its color is dark brown. Fertile structures are scattered over the blades but are not easily visible. *D. chathamensis* can be found in the low intertidal and upper subtidal zones, to ca. 2-m depth on exposed reefs in the Chatham Islands.

Durvillaea poha C.I.Fraser, H.G.Spencer & J.M.Waters 2012: 153, Figs. 2–5

Thalli perennial is up to 5–10 (12)-m long with the following characteristics: inflated, "honeycombed," buoyant lamina variably divided; solitary orange-yellow stipe, sometimes divided distally into several boughs, often not tapering with a concave cross-section; holdfast dense, discoid, and usually excavated by burrowing invertebrates; blades occasionally perforated; blades always flattened, never terete (cylindrical in cross-section). *D. poha* is found commonly at mid-tide level, on exposed rocky coasts, usually in a band above *D. antarctica*, and on semi-sheltered coasts throughout the intertidal zone.

Durvillaea potatorum (Labill.) Aresch. 1854: 343

Synonyms:

Fucus potatorum Labill. 1807

Sarcophycus potatorum (Labill.) Kütz. 1843

This species has the following characteristics: thallus dark brown, younger parts medium brown, usually 2–8-m long, with a massive discoid to broadly conical holdfast 5–25 cm across and 0.5–4-cm thick in mature plants, with a single (rarely 2–3 by fusion of holdfasts) stout, terete stipe (5–) 10–50-cm long, and 2–8 (–12) cm in diameter, usually without but occasionally with 1–2 proliferous laterals, bearing a divided, complanate, leathery frond with long segments, divided to near the base or to any position, usually (5–) 10–40-cm broad and 0.5–2-cm thick near the base, slenderer above with ultimate segments linear to gently tapering, usually 2–20-mm broad and 2–5-mm thick; blades often proliferous from the margins above the stipe, probably partly following damage. No internal honeycomb structure ("solid" bladed).

Durvillaea willana Lindauer 1949: 348, Fig. 6

Thalli grow up to 5-m long and consist of massive blades, tough, and leathery, sometimes divided into straps, with no internal honeycomb structure ("solid" bladed). Stipe is thick, cylindrical, and produces side branches (stipitate lateral blades). The specie holdfast a dome-shaped disc and its color is dark brown. Fertile structures are scattered over the blades but are not easily visible. *D. willana* is found in the low intertidal and upper subtidal zones, only on exposed coasts.

Distribution, ecology, and metabolism

Distribution

Durvillaea occurs only in the Southern Hemisphere. Most species are non-buoyant, and these have restricted geographic ranges, in some cases endemic to small oceanic islands. Buoyant members of the genus are more widespread, with one (*D. antarctica*) found throughout the subantarctic islands, and along the coasts of southern Chile and New Zealand.

Australia

Two species are found in Australia, and both are non-buoyant—they are *D. potatorum*, and *D. amatheiae*. *Durvillaea amatheiae* was described in 2017 (Weber et al. 2017) and earlier works referring to *D. potatorum* could therefore include research on the then-unidentified *D. amatheiae*.

In Australia, the recorded northern limit of *Durvillaea* is Tathra in southern New South Wales (*D. amatheiae* (Weber et al. 2017), previously recorded as *D. potatorum* at this location) (36° 43′ 33.56″ S, 149° 59′ 29.85″ E), although earlier records of a more northern limit suggest the kelp's range is shifting south (Millar 2007). Near its northern limit in Australia, populations are sparse and patchy (C. Fraser pers. obs). *Durvillaea* also grows abundantly along the eastern, western, and southern coasts of Tasmania, and in Victoria from the north-eastern border to Robe in the west. *Durvillaea potatorum* is quite abundant on King Island in Bass Strait (Cheshire and Hallam 1988b), where beach-cast plants are commercially harvested, but is scarce and patchy on the eastern islands in Bass Strait (J Luddington, Flinders Island Adventures, pers. comm.). There is a biogeographic break near Wilson Promontory, with *D. amatheiae* to the east and north, and *D. potatorum* to the west; at the current time, there is no evidence of the two species co-occurring on the mainland, although sampling has not occurred at a wide enough range of depths and sites to confirm the geographic delineation. In Tasmania, both species co-occur (Weber et al. 2017). Sites from which either species has been collected, with identity confirmed using molecular data (Weber et al. 2017), are shown in Fig. 1.

New Zealand

The majority of *Durvillaea* species (four named species and one unnamed species) are found in the New Zealand region. *Durvillaea chathamensis* and an undescribed but distinct species from the Antipodes Islands (see Hay 1994) are solid-bladed taxa that each occurs only on remote islands (Fig. 2). *Durvillaea willana* is also solid-bladed but has a wider distribution, growing around southern New Zealand (South Island and Stewart Island, and Castlepoint on the North Island) (Hay 1979b; Neale and Nelson 1998). New Zealand is also home to two buoyant species, *D. poha* and *D. antarctica* (Fraser et al. 2012). *Durvillaea poha* has a similar distribution to *D. willana*, recorded from Fiordland on the west coast of the South Island, along the east coast of the South Island (although not yet confirmed from north of Oaro, near Kaikoura), and on the subantarctic Snares and Auckland Islands (Fraser et al. 2009a, 2012). *Durvillaea antarctica* occurs along all New Zealand coasts, including subantarctic islands and the Chatham Islands (Hay 1979b; Fraser et al. 2010b), and along the west coast of the South Island (Neale

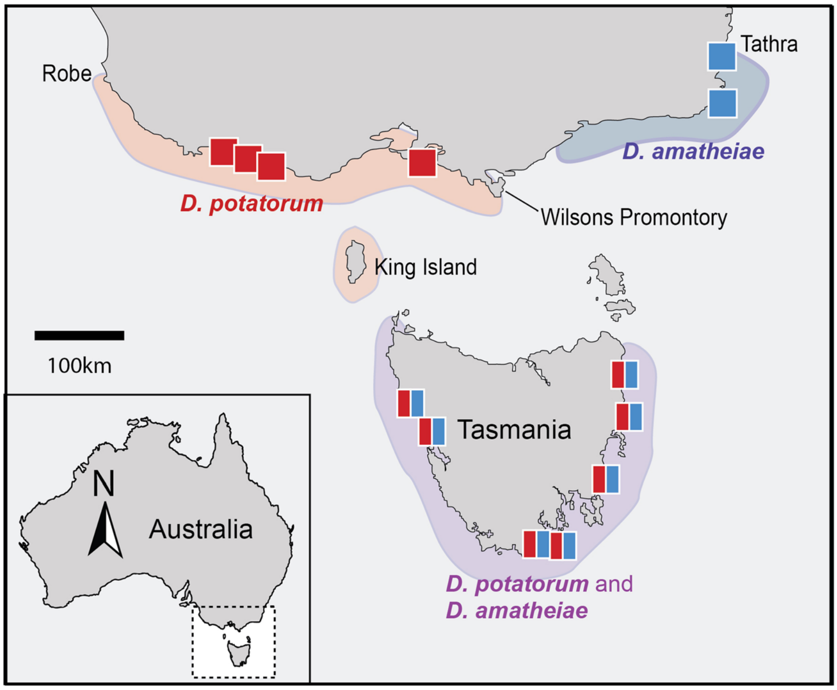


Fig. 1 Distributions of the two Australian *Durvillaea* species, with the inferred distribution of *D. amatheiae* shown in blue shading, and the inferred distribution of *D. potatorum* in red shading (purple where both are inferred to co-occur). Squares show sites from which genetic data have validated the presence of one or both species (based on Fraser et al. 2009c; Weber et al. 2017)

and Nelson 1998; Bussolini and Waters 2015). This species shows a phylogeographic break across the Canterbury Bight, with a genetically distinct "northern" lineage occurring from Banks Peninsula northward, including around the North Island (Fraser et al. 2010b; Bussolini and Waters 2015). The "northern" lineage also occurs at the Chatham and Bounty Islands.

The subantarctic

Durvillaea antarctica occurs throughout the subantarctic, mostly on islands to the north of the Antarctic Polar Front (APF), but also on non-glaciated coasts of Heard Island and South Georgia, which usually sit slightly to the south of the APF. Specifically, the species is known to grow in the New Zealand region (including the Snares, Bounties, and Antipodes Islands, Auckland Island and Campbell Island), as well as in the southern Indian ocean on Marion and Prince Edward Islands, the Kerguelen Islands, and Heard Island, and in the southern Atlantic Ocean on the Falkland Islands, South Georgia, and Gough Island (Hay 1979a, 1988; Fraser et al. 2009b). Populations genetically similar to those of the subantarctic occur along the southern Chilean coast (see next section).

Chile

Durvillaea antarctica is recorded along the coast of Chile, from Cape Horn in the south (56° S), to Coquimbo (30° S) in the north (Tala et al. 2013; Mansilla et al. 2017). Molecular analyses indicate a major biogeographic break to the south of Isla Betecoi (43° S) (Fraser et al. 2010a), with more southern, "Patagonian" populations grouping closely with subantarctic populations, and the more northern populations forming a deeply divergent clade (Fraser et al. 2010b) that probably represents a distinct species.

Dispersal

Durvillaea has a leptokurtic dispersal mode, with many gametes dispersing well over short distances, and relatively few adults dispersing longer distances (Fraser et al. 2018a). Fertilized eggs usually settle within a few (< 12) hours (Taylor and Schiel 2003) and within a few (usually 1–2, but sometimes > 8) meters of the parent (Dunmore 2006). Most dispersal between rock platforms must therefore be by detached, fertile adult thalli.

The non-buoyant species of the genus are thought to be poor dispersers, and this assumption is supported by high endemicity in solid-bladed taxa. In contrast, the species with inflated blades (*D. antarctica* and *D. poha*) are both robust and buoyant, and speculations that *D. antarctica* should be able to travel long distances at sea, carrying diverse flora and fauna (Edgar and Burton 2000; López et al. 2018), have been supported by recent molecular (Fraser et al. 2011) and ecological (López et al. 2017a, 2018) studies. High floating persistence (> 200 days) has been recently described in situ experiments at high latitudes (Tala et al. 2019). Indeed, the longest recorded biological rafting event was of floating *D. antarctica* traveling more than 20,000 km from the

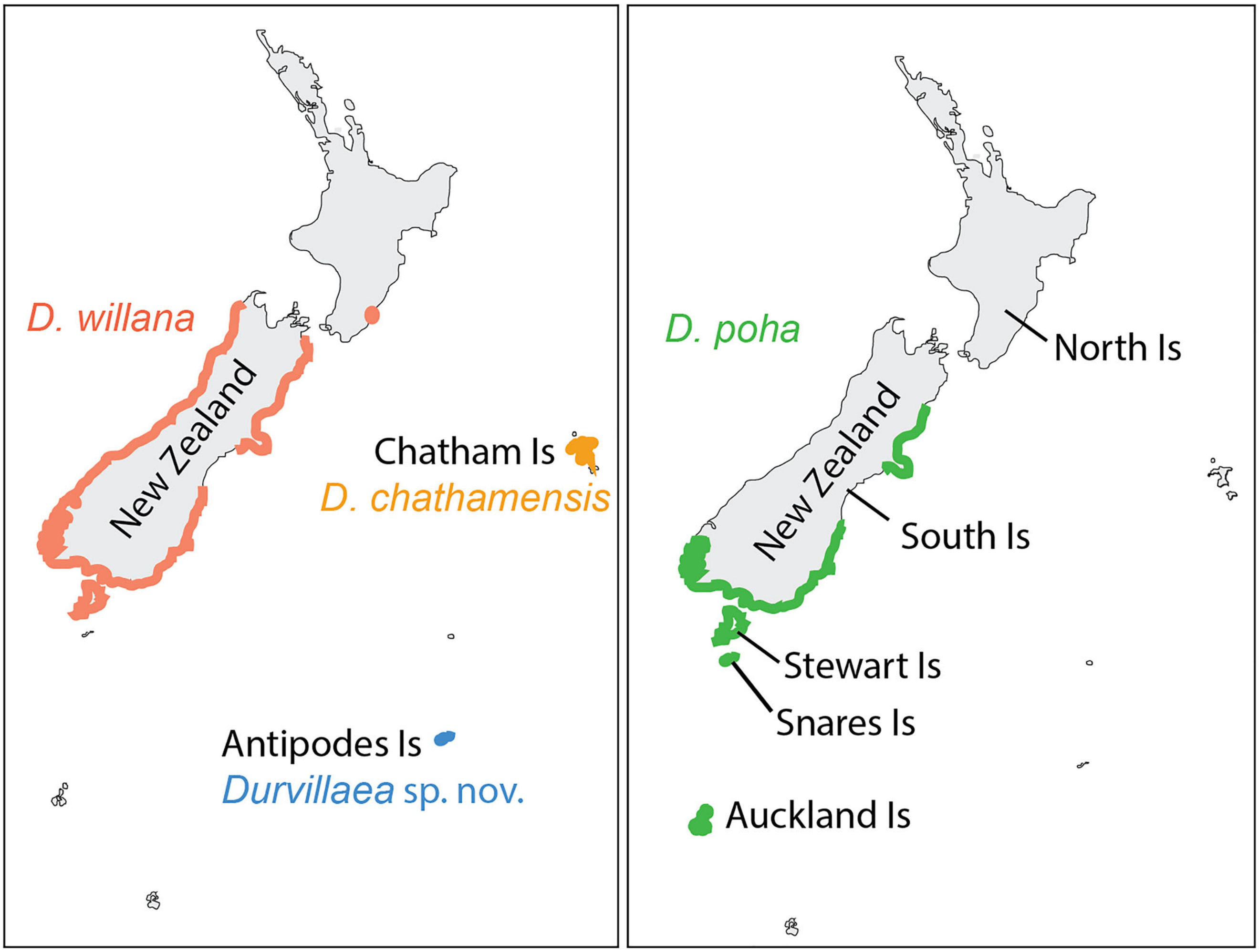


Fig. 2 Known distributions of *Durvillaea* species endemic to the New Zealand region. Not shown: *D. antarctica*, which grows throughout the region and in the subantarctic

subantarctic to Antarctica (Fraser et al. 2018b). *Durvillaea poha*, however, has wide blades and is therefore less streamlined and hydrodynamic than *D. antarctica*, which might help to explain its more restricted distribution.

Local vertical distribution

The New Zealand region

The solid-bladed taxa found in the New Zealand region all occur in the lower intertidal. *Durvillaea willana* and the undescribed species from the Antipodes Islands also extend a few (usually < 10) meter depth subtidally, whereas *D. chathamensis* only extends to the extreme low water mark of spring tides (Hay 1994).

On gently sloping, exposed rock platforms in southern New Zealand, *D. willana* forms a distinct band in the low intertidal, with *D. antarctica* just above it, and *D. poha* above that (Fig. 3). *Durvillaea poha* can also occur in the absence of *D. willana* or *D. antarctica*, in relatively sheltered locations such as inside the mouth of harbors and bays. Likewise, *D. willana* can occur in the absence of *D. antarctica* or *D. poha*, where only subtidal rocky habitats are available.

Physiological tolerances of the species dictate vertical distribution. Experimental removal of limpets from the intertidal band in the 1.6-m above *D. antarctica* allowed initial colonization by new recruits, but these did not survive through summer (Hay 1979c). Similarly, removal of *D. antarctica* was not found to enable an upward extension of *D. willana* (Hay and South 1979).

Australia

Intriguingly, preliminary data suggest that there could be a difference in vertical distribution between the two Australian species, as genetic data (COI sequences) from samples collected in 2010 from three sites in eastern Tasmania, where the species co-occur, indicate a greater proportion of *D. amatheiae* in subtidally collected samples and a greater proportion of *D. potatorum* in intertidally collected samples.

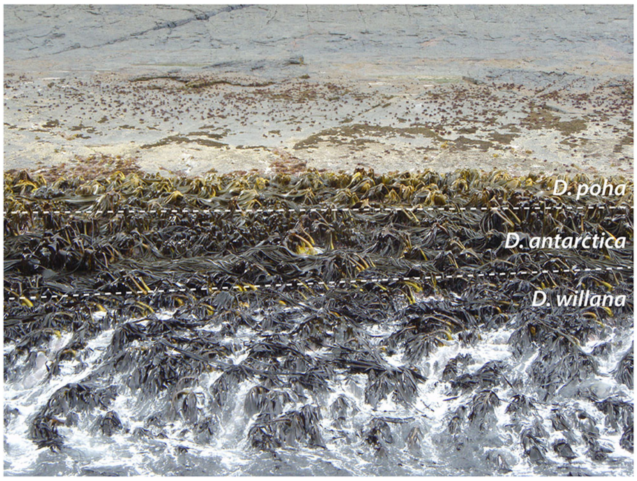


Fig. 3 Vertical distribution of the three fairly widespread *Durvillaea* species in southern New Zealand, on a gently sloping rock platform at Tautuku Peninsula. The predominant species occurring in each band is indicated

These results are shown here for the first time (Fig. 4) but are based on low sample numbers; future studies should aim to test whether this anecdotal observation represents a true pattern in the field.

The subantarctic and Chile

Only *D. antarctica* grows in the subantarctic and in Chile (although with a distinct genetic lineage in the northern part of its range: see above), and this species occurs mainly in the intertidal. Morphological variants of the species can occasionally occupy different depths, however. For example, solid-bladed morphotypes of *D. antarctica*, that can extend several meters into the subtidal zone, have been recorded (sometimes, historically, as distinct species) from subantarctic environments including Gough Island (see Hay 1994), Macquarie Island (see Klemm and Hallam 1988a), Falkland Islands (M. Clayton pers. comm.), and subantarctic region of Chile (Méndez et al. 2019). None of these, however, shows notable genetic differences to sympatric individuals with honeycombed blades (Fraser et al. 2010b). Similarly, wide-bladed, honeycombed individuals resembling *D. poha* have been observed in the intertidal in southern Chile (Méndez et al. 2017) and the Falkland Islands (C Fraser pers. obs.: Fig. 5), but these also do not show notable genetic differences with sympatric *D. antarctica* (unpublished mitochondrial COI data, C. Fraser).

Environmental requirements

All *Durvillaea* species require rocky substrate for attachment and wave-exposed environments (Hay 1994). High turbulence promotes high biomass for *D. potatorum*, and probably for other species in the genus, presumably because fronds are constantly turned (allowing pulses of light to reach photosynthetic surfaces), wastes are rapidly removed, and the supply of nutrients and gases refreshed (Cheshire and Hallam 1988a). *Durvillaea* does not occur on coasts subjected to frequent ice

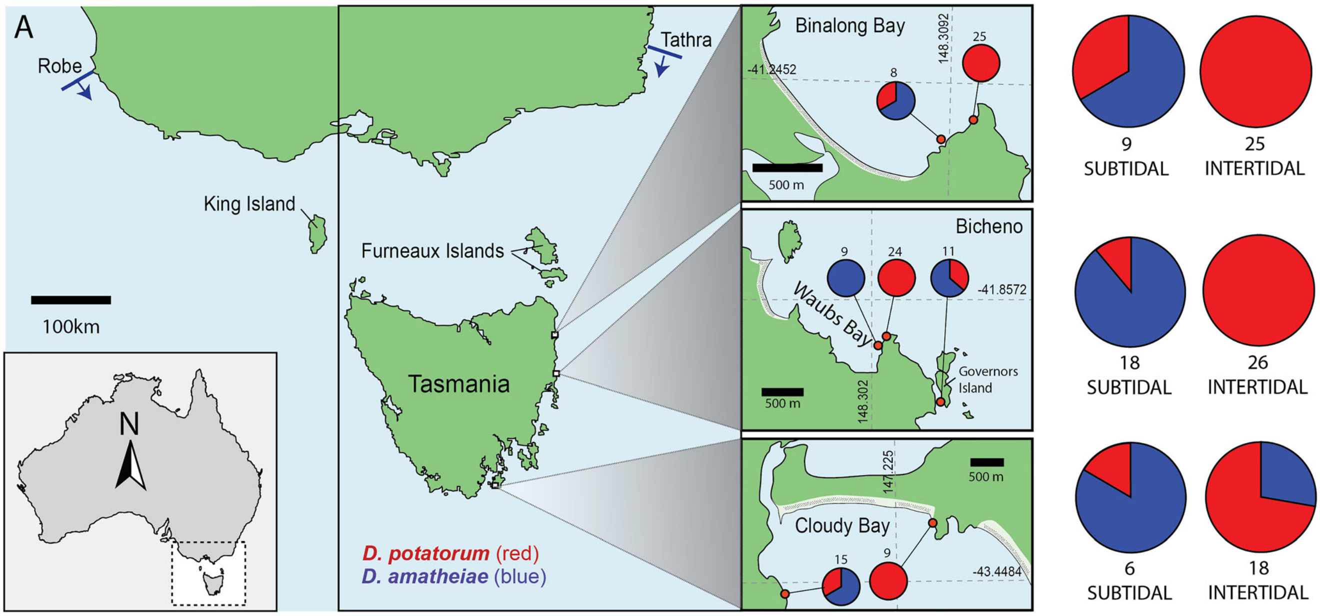


Fig. 4 mtDNA analyses of *Durvillaea* from the eastern coast of Tasmania in 2010 suggest that the two species might have depth differences: *D. potatorum* (red) was more often found in the intertidal, and *D. amatheiae* (blue) was more often found in the subtidal. These samples were collected before the species' morphological differences had been identified, however, and need to be confirmed by more detailed ecological assessments

Fig. 5 Morphotypes of *D. antarctica* in the Falkland Islands can resemble *D. poha* in New Zealand, with wide blades and short, stout stipes but have not been found to be genetically distinct. Photo: C. Fraser, Falkland Islands, 2008

scour, for example, where glaciers and icebergs reach the shore (Hay 1988), and is thought to have been removed from most subantarctic islands by ice scour at the Last Glacial Maximum (Fraser et al. 2009b). *Durvillaea* grows in cold and cool-temperate waters, and although its southern limit is probably limited by ice scour rather than low temperature (Fraser et al. 2018b), its northern limit is thought to be temperature-dependent. In Australia, for example, the northern limit of *D. potatorum* is shifting south, presumably as a result of ocean warming (Millar 2007).

Environmental stressors

Durvillaea antarctica can survive and continue to photosynthesize when detached from its substrate, but drifting individuals are generally less healthy than attached, particularly during summer/at higher temperatures (Cruces et al. 2012, 2013; Tala et al. 2013, 2016, 2019). Some pollutants might have damaging effects; high levels of copper, for example, have been found to inhibit photosynthesis for *D. antarctica* in Chile (Huovinen et al. 2010). Recently, extensive mortalities were reported in New Zealand (South Island) due to the strongest marine heatwaves recorded in the last 38 years; seawater temperatures near 23 °C and air temperatures above 30 °C were recorded, producing 100% loss of *D. poha* at Pile Bay (44°S) but also affecting populations of *D. willana* and *D. antarctica* (Thomsen et al. 2019).

Growth

Growth of *Durvillaea* occurs in the meristoderm (the outermost layers of the thallus), via division of meristodermal cells, with a single cell creating multiple cells on the outer layer (summarized by Hay 1994). Growth in *D. antarctica* and *D. willana* in New Zealand was found to be most rapid in small individuals and slowest in large individuals and in winter (Hay 1994). Although detached, *D. antarctica* suffers in warm, low-latitude waters; at high latitudes, survival and health of drift individuals can be enhanced, and growth can continue (Tala et al. 2016, 2019). Shading of *D. antarctica* by other seaweeds, especially on gently sloping rocky shores, can slow growth rates (Hay 1994). Nonetheless, growth is usually rapid in this genus, and *D. antarctica* can be as much as 4 m in the first 2 years (Hay 1994).

Life history

Life cycle

Alternation of generations

Durvillaea spp. have a diplontic life cycle, lack a free-living gametophyte, and have oogamous reproduction (Fig. 6) (Maier and Clayton 1989; Collantes et al. 2002).

Reproduction

Durvillaea spp. have high reproductive potential (Clayton et al. 1987; Hay 1994); an individual can release 120 million ova in a single night (Hay 1994). Sexual reproduction is oogamous, with dioecious individuals. Gametes are produced in conceptacles scattered over the blade. Male individuals produce antherozoids (motile flagellate gametes) through successive meiosis, while female individuals have conceptacles that contain multiple larger oogonia, with four large, oospheres within each oogonium (Maier and Clayton 1989; Hay 1994).

Fertilization can be achieved by mixing eggs and sperm in sea water (Hay 1994; Collantes et al. 2002). Ten hours after the fertilization, the zygote develops a thick wall. A slight protrusion begins to develop, and a large part of the oosphere becomes pear-shaped. The protuberance becomes a primary rhizoid and, ultimately, a cluster of rhizoids. After 24 h, a septum appears that divides the zygote into unequal cells with the smallest cell at the rhizoid end. The larger cell divides transversely again, and the upper part of these cells divides longitudinally. After 72 h, most germlings comprise three or four cells. The divisions of the largest initial cell eventually form a slightly flattened, oval or approximately 100-m-long body. The thick wall that originally encapsulated the zygote remains as a curved "cap." The cells derived from the smallest cell of the first division are divided less frequently than those derived from the larger one. At 9 days, a primary rhizoid of three or four cells begins to branch. After about 2 to 3 weeks, up to three rhizoids are formed and the body of the young thalli is placed in an upright position. The rhizoids of the adjacent zygotes intertwine a lot but do not seem to merge.

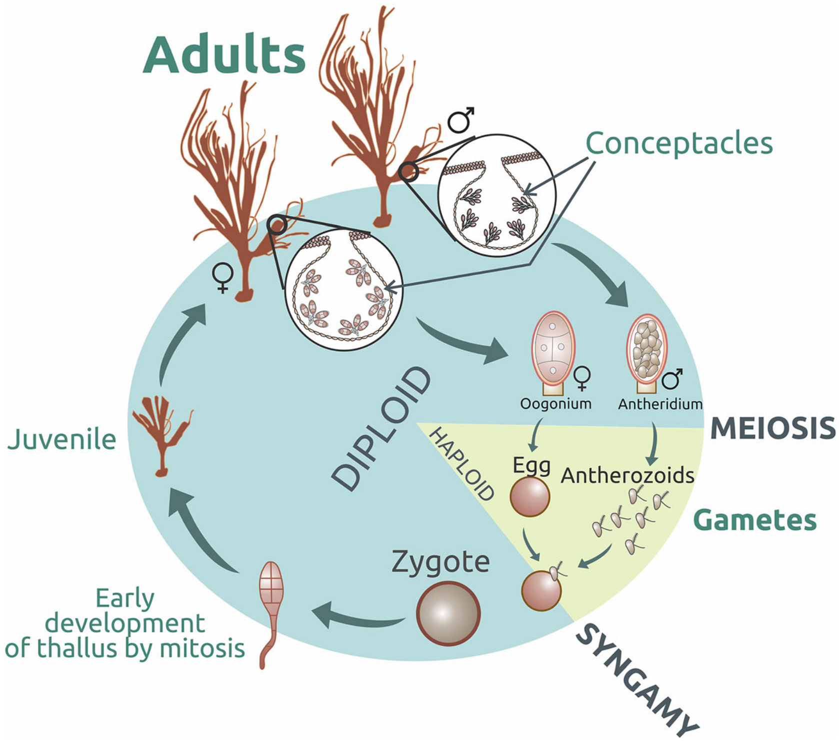


Fig. 6 Life cycle of *Durvillaea* spp. © E. Macaya

Thus, compound holdfasts can be formed at this very early stage. After 6–8 weeks in culture, the erect portions of the juvenile thalli can be 1 to 2-mm long; at which stage, it is best to transplant these developing thalli to a free-flowing seawater system to ensure further development.

Phenology

Seasonal variation in external appearance and morphology

Along the Chilean coast two types of *Durvillaea* species with different colors are recognized, known as "black cochayuyo" and "blonde cochayuyo." The black color appears to be common during the coldest season, while during the months of high solar radiation, direct exposure changes the color of the black thallus to a light blond, which is believed to affect the nutritional composition of the cochayuyo. The "blonde cochayuyo" corresponds to a lower-quality product for direct human consumption and the "black cochayuyo" of better quality that is exported (Ávila et al. 2005). Slight color differences have been described between vegetative and reproductive sexual stages (Lizée-Prynne et al. 2016).

Seasonal variation in biomass and reproduction

Durvillaea populations consist of male and female thalli. Vásquez et al. (2008) found in central Chile a similar proportion of male and female thalli (among mature and senescent individuals) in autumn and winter, and they also described a high frequency of vegetative individuals during summer. Similarly, Westermeier et al. (1994) found that, in central Chile, *D. antarctica* populations were dominated during summer and autumn by vegetative individuals (more than 80%). In populations of *D. antarctica* from Magallanes, Mansilla et al. (2017) reported a high proportion of male individuals in summer with some small increase of females towards autumn and winter.

In general, *D. antarctica* shows a pattern of seasonal variation of reproduction, with the maximum reproductive individuals in winter and with few or no reproductive individuals occurring during summer (Klemm and Hallam 1988b; Hay 1994; Collantes et al. 2002; Tala et al. 2016, 2019). However, a recent long-term study suggests that populations of *D. antarctica* from subantarctic Chile (> 54°) are reproductive throughout the year and reach their maximum reproductive peaks in autumn, declining gradually towards summer (Mansilla et al. 2017).

Populations

Structure

Age composition

The age of *Durvillaea* has been studied using the layering of conceptacles; in some thalli, those senescent conceptacles become occluded by ingrowth of hyphae and then buried (annually) in the cortex (Naylor 1953). Collantes et al. (2002) described individuals of *D. antarctica* from central Chile with two layers of conceptacles being at least 2 years old. However, the number of conceptacle layers can be variable according to biotic or abiotic conditions (Collantes et al. 2002) and also will depend on how long it takes for an individual to become fertile.

Longevity in *Durvillaea* is not known although according to Hay (1979d); some individuals can probably live up to 10 years. Large individuals of *D. potatorum* in Victoria, Australia, may live for 7 or 8 years, growing up to 10 m in length (Clayton et al. 1987). According to Hay (1977), size in *Durvillaea* often bears no relationship to age.

Size composition

Stipe length for *Durvillaea* has been used as a proxy for biomass (Table 1), e.g., stipes with a length of 16 cm or more include thalli of 10 to 20 kg (Hay 1977). Cheshire and Hallam (1989) used the stipe circumference and maximum length to evaluate the population composition of *D. potatorum*, where thalli with stipe circumferences from 10 to 39 mm were considered juveniles, whereas stipes from 40 to > 120 mm were considered to represent adult thalli.

Size structure in thalli of *D. antarctica* from central and southern Chile is highly variable depending on harvesting intensity and management plans, in the absence of harvesting. It depends on biotic and abiotic factors, such as competition with *Lessonia* species, herbivory, and nutrients (Santelices et al. 1980; Westermeier et al. 1994). In exposed sites in Chile with high *Lessonia* density, *D. antarctica* do not grow more than 150 cm, while in less exposed sites and low *Lessonia* density, they can reach up to 425 cm (Vásquez et al. 2008).

Abundance

Density of *Durvillaea* populations is usually determined by counting the holdfasts by area. However, coalescent holdfasts in *D. antarctica* are not uncommon (González et al. 2015; Lizée-Prynne et al. 2016; López et al. 2017a). The density of *D. antarctica* populations has been studied along the Chilean coast (e.g., Santelices et al. 1980, Westermeier et al. 1994; Ávila et al. 2005; Castilla et al. 2007; Vásquez et al. 2008), New Zealand (Hay 1979d; South and Hay 1979), Australia (Cheshire and Hallam 1988a), Kerguelen (Lawrence 1986), Macquarie Island, and Heard Island (Klemm and Hallam 1988b).

Maximum density values have been reported from central Chile by Westermeier et al. (1994) reaching up to 30 adults m^{-2} for *D. antarctica*, and similar values (21.6 adults m^{-2}) were observed in central Chile during January (Ávila et al. 2005). On Macquarie Island, up to 233 thalli m^{-2} were found, including juveniles and adults (Klemm and Hallam 1988b). Local density differences are determined by a number of biotic (e.g., competition) and abiotic factors (wave exposure, temperature, and harvesting (Santelices et al. 1980; Cheshire and Hallam 1988a; Westermeier et al. 1994; Vásquez et al. 2008).

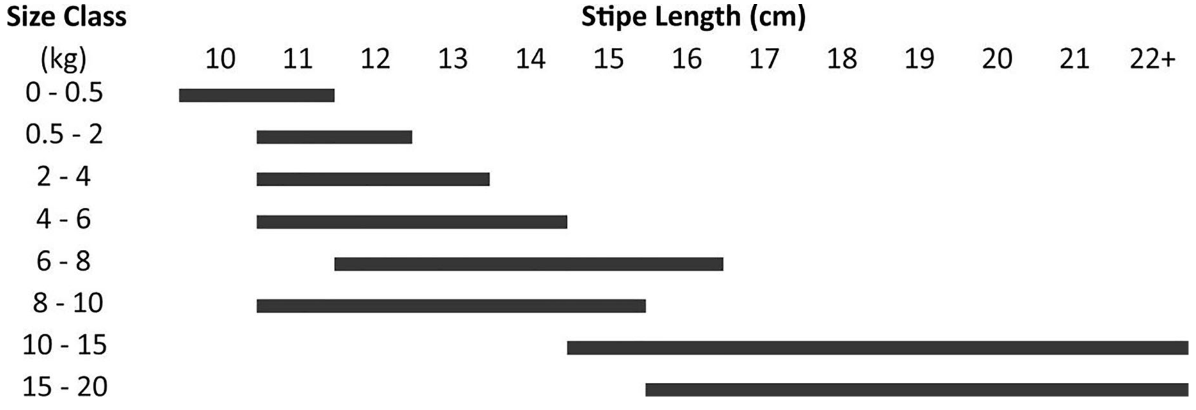
Standing stock

As far as we know, the only estimation of total biomass available (standing stock) of *Durvillaea* was carried out by Haxen and Grindley (1985) for Macquarie Island using aerial photographs, with a total estimated of 330,000 kg (*w/w*). On the other hand, Smith (2002) estimated 70 million *D. antarctica* rafts floating at any time in the Southern Ocean; 28.6% of those having holdfasts still attached. Klemm and Hallam (1988b) estimate maximum values of 107 kg/m^2 as standing crop for the East Coast at Macquarie Island and 242 kg m^{-2} was estimated for West Bay at Heard Island, whereas Lawrence (1986) estimated 264 kg m^{-2} at Kerguelen Island.

Accompanying species

Several studies have investigated the organisms associated with *Durvillaea* (Cancino and Santelices 1980; Santelices et al. 1980; Haxen and Grindley 1985; McLay and Hayward

Table 1 Range of stipe length in successive size classes Modified from Hay (1977)



1987; Smith and Simpson 1995, 1998; Vásquez et al. 2008; Macaya et al. 2016; López et al. 2018). Holdfasts of *D. antarctica* have few exclusive species, and most of the fauna and flora can also be found inhabiting the rocky interstices nearby (Vásquez et al. 2008). Crustaceans are the most common group of invertebrates found in stranded (López et al. 2018) and benthic *Durvillaea* holdfasts (Santelices et al. 1980; Smith and Simpson 1995; Vasquez et al. 2008).

In a study along the continental coast of Chile, López et al. (2018) reported 89 species associated with holdfasts of stranded *D. antarctica*. Most of the associated organisms were seaweeds (71.9%) followed by invertebrates (28.1%). Some of the species were found up to 300 km outside of their known geographic range; therefore, the dispersal of some of these benthic species can be facilitated by rafting on *D. antarctica* holdfasts. Several studies have provided evidence of long-distance dispersal of intertidal species associated with floating *D. antarctica* (e.g., Donald et al. 2005; Nikula et al. 2010, 2011; Haye et al. 2012; López et al. 2017b). In Chile, some of the most common seaweeds associated with stranded holdfasts of *D. antarctica* are *Lessonia spicata*, *Corallina officinalis var. chilensis*, and *Gelidium lingulatum* (Macaya et al. 2016; López et al. 2018).

Few epiphyte and endophyte parasites have been described in *Durvillaea*. The parasitic endophyte *Herpodiscus durvillaeae* has been recorded in association with *D. antarctica* (South 1974; Heesch et al. 2008) and recently in *D. poha* and *D. willana* (Fraser and Waters 2013). An obligate phytomyxean parasite (Rhizaria), *Maullinia*, has been described infecting *Durvillaea* from Chile, Falkland Islands, Australia, and Marion Island (Blake et al. 2017; Murúa et al. 2017).

Holdfast communities in *D. antarctica* have been used to evaluate the impact of anthropogenic perturbation. Samples collected in Macquarie Island 7 years after an oil spill had holdfasts dominated by opportunistic worms (Smith and Simpson 1998).

Harvesting

Equipment and method of harvesting

Australia

Storm cast *D. potatorum* is harvested on King Island, Bass Strait, and also along the coast of South Australia. Harvesting is by hand collection and sometimes assisted by winches, and in some instances, a mechanical harvester with a mechanical grab may be used. Harvesters select the beach-cast thalli, leaving at least 50% of the biomass on the beach. Thalli are initially air-dried and then further dried to enable milling into a granular form (PIRSA 2014, http://www.kelpind.com.au/).

New Zealand

There is no commercial harvest of *Durvillaea* spp. in New Zealand.

Chile

Durvillaea antarctica is harvested along the whole coast of continental Chile from 29° S to 42° S. Harvesting is by hand in the intertidal leaving the holdfast (Fig. 7) and it represents the major proportion of the biomass collected in Chile. Artisanal fishermen use tools such as a corvo, a rod of 3 to 4-m long at the end of which is a knife shaped like a steel half-moon accompanied by a hook to drag the cut seaweed (Ávila et al. 2005). In addition, beach-cast thalli are harvested. Thalli are usually sun dried, although some parts (stipe) are used raw and fresh for human consumption.

Harvesting seasons

Australia

Harvesting of beach-cast *D. potatorum* occurs throughout the year but is dependent on prevailing weather conditions (PIRSA 2014).

Chile

Harvesting occurs during the whole year, but less biomass is collected from May to September because of the weather conditions (SERNAPESCA 2017).

New Zealand

Durvillaea spp. are not harvested commercially. Harvest trials have been conducted enabling some observations of the

Fig. 7 Harvesting of *D. antarctica* in central. Chile. Photo: E. Macaya, Biobío Region, 2018

impacts of harvest practices, on the biology and ecology of *D. antarctica*, for example, Hay and South (1979) concluded that harvesting whole thalli in autumn and early winter (April–July), prior to and during the fertile period of *D. antarctica* (May–October), resulted in much more successful recruitment than harvesting in summer, when other species colonized the bare substrate. Holdfasts of *Durvillaea* spp. persist for months on the rocks, preventing the successful settlement of new sporelings (Hay 1994).

Regrowth on harvested areas

Regrowth of *D. antarctica* was observed in Central Chile by Ávila et al. (2005). They studied the regeneration of individuals after cutting off the stipe immediately above the holdfast and at the end of the cylindrical portion. In both cases, regrowth was possible but only when cuts were carried out during March and September. After 7 months, plants regenerated more than 1 m of the blade. Harder et al. (2006) also suggested that broken tips of *Durvillaea* thalli can regrow. This capacity of regeneration of the individuals varied according to the season, with a better response during spring than autumn.

Total annual yields

Australia

Harvest quantities have varied considerably over the history of the *D. potatorum* kelp industry, influenced not only by storms and availability of beach-cast material but also market demands. The average harvests of *Durvillaea* at King Island in the last 10 years have been around 2,500,000 kg year^{-1}, with maximal harvest of 4,700,000 kg year^{-1}. In South Australia, the maximum macroalgal harvest rates have not exceeded 305 t in any year, with average harvest rates of < 79 kg kg year^{-1} (PIRSA 2014).

Chile

In Chile, over the past ca. 37 years, the harvest of large brown algae has fluctuated between 4,000,000 and 39,000,000 kg year^{-1}, showing a sustained increase since 2000 (Fig. 8). Vásquez (2016) reported that the kelps *Lessonia nigrescens*-complex (mainly *L. berteroana*) and *L. trabeculata* comprise more than 90% of the total production, and *Macrocystis* and local consumption of Durvillaea *antarctica* contribute only marginally to total landings (Vásquez 2016; www.sernapesca.cl).

Protection and management

Official regulations

Australia

Only beach-cast thalli of *D. potatorum* are harvested, based on the reasoning that "the direct life history strategy of Durvillaea is not suitable for a live harvest. In species with a direct life history the reproductive potential of the plant is stored in the standing biomass and any cutting of attached plants would have a major impact on the persistence of the harvested populations. Similarly, the diffuse but largely apical meristem in *Durvillaea* means that the major growing portion of the plant is the proximal region of the thallus and cutting would remove this material and thereby restrict growth of any remaining plant material." (PIRSA 2014).

Harvesters require harvesting licenses for the King Island *D. potatorum* industry. In 2014, there were 100 registered

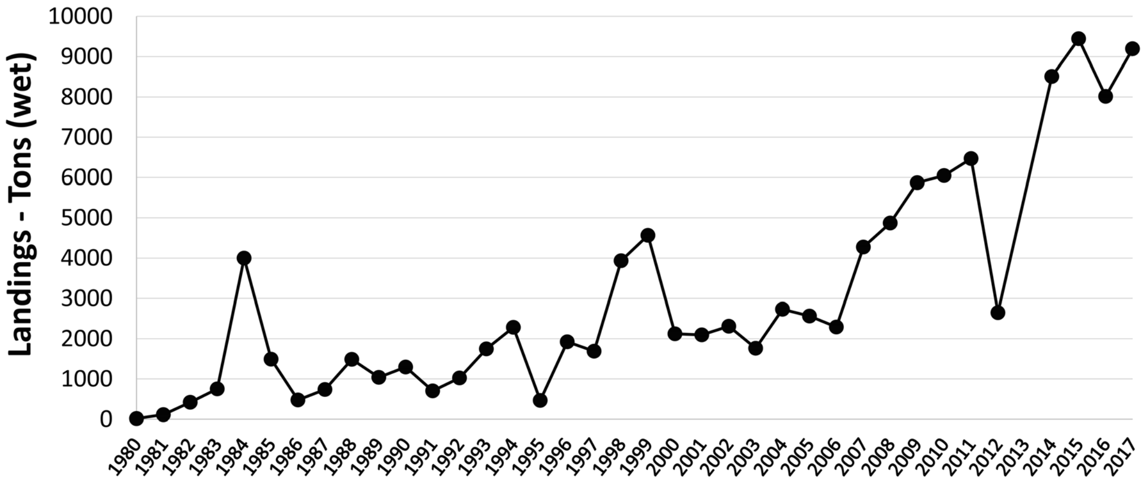


Fig. 8 Landing *D. antarctica*—Chile. Data from Sernapesca 1980–2017

licenses, four of which were full-time collectors, 40 part-time, and the remainder inactive. Kelp Industries Pty Ltd. is the only licensed processor of kelp on King Island. Kelp Industries works to a collector's code of conduct as well as the Tasmanian Living Marine Resources Management Act 1995. The Department of the Environment and Heritage (DEH) produced an "Assessment of the Harvest of Cast Bull Kelp" (DSEWPaC 2011). Currently, native seaweeds in Tasmania are not directly harvested due to their ecological importance to marine ecosystems and fisheries resources (PIRSA 2014).

In South Australia in 2014, there were two operators with licenses, issued under the *Fisheries Management Act 2007*. The commercial harvesting of beach-cast seaweed, or wrack, from any beach of the State of South Australia is under the care, control, and management of PIRSA (Primary Industries and Regions SA) Fisheries and Aquaculture on behalf of the community in accordance with the Act. The Act provides a broad statutory framework to ensure the ecologically sustainable management of South Australia's aquatic resources. The regulations that govern the management of the South Australian Beach-Cast Seagrass and Marine Algae Fishery are the *Fisheries Management (Miscellaneous Fishery) Regulations 2000* and the *Fisheries Management (General) Regulations 2007* (PIRSA 2014).

New Zealand

The harvest of *Durvillaea* species in New Zealand is controlled by the Fisheries Act (1996). Under Section 93 of the Act, species listed in Schedule 4C are subject to a permit moratorium. Schedule 4C includes *Durvillaea* spp. from Fisheries Management Areas 1–10 (throughout the country). The moratorium on the issue of new fishing permits for seaweeds was imposed in 1988 and under present legislation, no new entrants can gain access to the industry (Zemke-White and Ohno 1999).

In addition, under the Ngai Tahu Claims Settlement Act 1998, the commercial harvest of bull kelp (*Durvillaea* spp.) is totally prohibited in the Challenger/south-east/Southland and subantarctic areas of New Zealand. Within Te Roroa (Northland), with respect to *Durvillaea*, the Minister of Fisheries is required to ensure that the customary non-commercial fishing interests of Te Roroa are recognized and provided for when considering the setting of any Total Allowable Catch or Total Allowable Commercial Catch.

Chile

Approximately 50% of marine landings in Chile are based on artisanal kelp harvesters operating in coastal zones (Castilla 2010). The legal framework (Fisheries and Aquaculture Law No 18.892) that regulates fisheries in Chile provides a series of management policies such as marine zoning, including allocating exclusive territorial users rights for fisheries (TURFs), and establishing management plans (Castilla 2010). The TURFs policy implemented in Chile takes the form of Management and Exploitation Area for Benthic Resource policy (Castilla et al. 1994), by which exclusive access diving rights are assigned to organizations by the undersecretary of fisheries (Castilla et al. 1998; Gelcich et al. 2010). Gelcich et al. (2015) outline the rationale for establishing TURFs, which are based on common-property and co-management theories that consider "securing access and sharing control over resources can create incentives for sustainable institutional arrangements among fishers, who will then manage and fish collectively and sustainably". *Durvillaea antarctica* (Cochayuyo) is included in TURF management plans (Advanced Conservation Strategies 2011). Extraction from natural populations outside TURF is regulated in Chile with ban periods and/or harvest quotas (SUBPESCA).

Customary Fisheries

Australia

Thurstan et al. (2018) have assessed the use of seaweeds by indigenous Australians based on archival records. From the information currently available, *D. potatorum* had the "broadest reported application, with uses in roofing material for shelters, footwear, moulding of cups and water-carriers, and a 'highly nutritious' food that was suitable for preservation and transport". Records of eating *D. potatorum* indicate that this species was prepared by "initial sun-drying, followed by careful roasting over a fire where it was turned frequently and then finally soaking for 10–12 h in freshwater before eating alone or with meat or fish". Once prepared in this manner, it could be preserved for many months.

There are records dating to as early as 1791 of baskets for carrying water being constructed from *D. potatorum* (Mortimer 1791), which Thurstan et al. (2018) report is a craft that continues today.

New Zealand

Pōhā are bags made of hollowed, inflated blades of *Durvillaea*, enclosed in strips of tōtara bark and placed in flax kete (baskets). Tītī or muttonbirds are harvested from Rakiura (Stewart Island) by Rakiura Māori under the Tītī (Muttonbird) Islands Regulations 1978 and were traditionally stored in pōhā surrounded by fat from the birds (https://teara.govt.nz/en/titi-muttonbirding). A video is available explaining the preparation of pōhā tītī and their continued use: http://www.maoritube.co.nz/people/poha-bull-kelp-bags-ngai-tahu-mahinga-kai/, and an application to assist birders harvesting tītī to manage the resource has also been produced: [http://

www.maramatanga.ac.nz/sites/default/files/Te%20Poha%20o%20Te%20Titi%20User%20Manual.pdf].

Chile

Durvillaea antarctica has been used for human consumption in Chile by the Mapuches since pre-Columbian times and later by modern intertidal subsistence food-gatherers and fishermen (Bustamante and Castilla 1990; Castilla et al. 2007). Archeological evidence in Monte Verde, Southern Chile, suggests the use of *D. antarctica* and other seaweeds for about 14,000 years as food and medical purposes (Dillehay et al. 2008). The stipe (called "ulte" or "huilte") and the dried blades (called commonly "cochayuyo" or "kollof" in Mapudungun) are consumed and sold in local markets (Fig. 9). Chemical analysis has demonstrated a high content of proteins, essential amino acids, vitamins, and dietary fibers (Ortiz et al. 2006). For more information, see the "Chemical composition" section.

Today, *D. antarctica* has become a "superfood" in the Chilean market, and a variety of products have been developed such as cookies, burgers, cereal bars, several flavored snacks, and jam, among others. It has been also incorporated and mixed with flour (Fig. 9) and is sold in different formats (e.g., ground, cut into small pieces "brunoise").

Chemical composition

As brown seaweeds, *Durvillaea* species are chemically characterized by the photosynthetic pigments chlorophyll *a* and *c* as well as fucoxanthin, which serves as the main carotenoid accessory pigment. Alginate and fucoidan are the major structural components in the cell walls, and fucosterol is the most important sterol while phlorotannins serve as secondary metabolites. Information about the biochemical composition of *Durvillaea* species are usually related to concentration and composition of alginate, together with their nutritional values (e.g., proximal, fatty acids and amino acids profiles, minerals) and with ecophysiological traits (e.g., pigments and phlorotannin concentrations) associated to environmental changes under benthic and floating conditions (Table 2). From the six recognized species, *D. antarctica* is the species with the highest number of studies, describing some aspect of its chemical composition mainly from populations of Chile and New Zealand (Table 2). Multiple factors affect the biochemical concentration and composition of seaweed species such as age, size, season, habitat, abiotic conditions (light intensity, water temperature, and nutrient availability), and biotic conditions (herbivory pressure and pathogens) (Mabeau and Fleurence 1993; Hafting et al. 2015).

Fig. 9 Different products from *Durvillaea antarctica* sold in Chilean markets

Table 2 Chemical characteristics studied in *Durvillaea* species including conditions (time, tissue type, age) and location

Species	Chemical variable(s)—tissue	Conditions	Location	References
D. potatorum	Alginate	Benthic thallus and 7 thallus zones in blade, stipe, and holdfast May 1981	Victoria, Australia 37° S–144° E	Cheshire and Hallam (1985)
D. antarctica	Sulfated polysaccharides rich in fucose	Benthic thallus Early spring (Sep)	Pelancura, Chile 33° S–71° W	Matsuhiro et al. (1996)
D. antarctica *D. potatorum* *D. willana*	Alginate, composition, and structure	Benthic thallus, only blade tissue Spring (Nov)	Dunedin, South Island New Zealand 45° S–170° E	Panikkar and Brasch (1996)
D. antarctica *D. willana*	Alginate, composition, and structure	Benthic thallus considered blade and stipe Bimonthly samples (Mar 1990–Mar 1992)	Dunedin, South Island New Zealand 45° S–170° E	Kelly and Brown (2000)
D. potatorum	Alginate, crude fiber, protein, ash, minerals (phosphate, sulfate, iodide, and chloride), chlorophyll *a* and *c*, phenolic compounds, laminarin, fucoidan, and mannitol	Benthic thallus Mid-April (autumn)	Without information	Madgwick and Ralph (1972)
D. antarctica	Nutritional composition (energy, ash, protein, lipid, soluble, and insoluble carbohydrates)	Benthic thallus separated in blade, stipe, and holdfast Spring (Dec 1984) Sheltered shore	Bay of Morbiham, Kerguelen 49° S–70° E	Lawrence (1986)
D. antarctica	Nutritional composition (energy, ash, protein, lipid, soluble, and insoluble carbohydrate)	Benthic thallus separated in blade, stipe, and holdfast of recruits, juveniles, and adults Monthly samples	Mehuin, Chile 39° S–73° S	Westermeier (1987)
D. potatorum	Lipid class, fatty acid, and sterol profiles	Commercially dried, fresh, and beach-cast bull kelps	Tasmania (Nov 1993)	Virtue & Nichols (1994)
D. antarctica	Nutritional composition (moisture, ash, proteins, lipids, carbohydrates, dietary fiber), amino acid and fatty acid profiles, tocopherols, and tocotrienols.	Benthic thallus separated in blades and stipes. Without information about sampling time	Central Chile (~ 35° S)	Ortiz et al. (2006)
D. antarctica	Nutritional composition, minerals, and metals (Iron, calcium, sodium, potassium, manganese, phosphate, zinc, cooper, selenium, chloride, iodide, mercury, arsenic, lead)	Benthic thallus	Auckland, New Zealand (36° S–174° E) (April 2004)	Smith et al. (2010)
D. antarctica	Nutritional composition (carbohydrates, proteins, lipids), sodium and fatty acid profile	Cooking seaweed (bread, hamburgers, fettuccine) Oct–Dec 2012 (spring)	Pta. Arenas, Chile 53° S–70° W	Astorga-España et al. (2017)
D. antarctica	Nutritional composition (energy, ash, protein, lipid, soluble, and insoluble carbohydrates)	Drying temperature effects over blades Without information of sampling time	Pto. Oscuro, Northern Chile 31°–71° W	Uribe et al. (2017)
D. antarctica	Phlorotannins and antioxidant activity	Experimental lab conditions with juvenile pieces of bull kelp blades exposed to UV-radiation and temperature Spring (Oct) 2011 Summer (Dec) 2012	Valdivia, Southern Chile 39° S–73° W	Cruces et al. (2012, 2013)
D. antarctica	Pigments (chlorophyll $a + c$, carotenoids), phlorotannins	Benthic and floating thallus	Coquimbo (29° S–71° W), Chile	Tala et al. (2013)
D. antarctica	Pigments (chlorophyll $a + c$, carotenoids), phlorotannins	Benthic and floating thallus Winter 2013 (Jul–Sep), Summer 2013/2014 (Dec–Feb).	Coquimbo (29° S–71° W), Concepción (36° S–72° W), Pta. Arenas (53–70° W), Chile	Tala et al. (2016)
D. antarctica	Pigments (chlorophyll $a + c$, carotenoids), phlorotannins	Benthic thallus of female and male samples	Pto. Oscuro and Totoralillo Sur, Chile 31–32° S–71° W	Lizée-Prynne et al. (2016)
D. antarctica	Pigments (chlorophyll $a + c$, carotenoids), phlorotannins		Coquimbo (29° S–71° W), Chile	Tala et al. (2017)

Table 2 (continued)

Species	Chemical variable(s)—tissue	Conditions	Location	References
		Experimental lab conditions with floating pieces of blades Late spring (Nov 11) and summer (Jan 12)		
D. antarctica	Pigments (chlorophyll *a* + *c*, carotenoids)	Two benthic floating and non-floating morphotypes	Pta. Arenas, Chile 53° S–70° W	Méndez et al. (2017)
D. antarctica	Pigments (chlorophyll *a* + *c*, carotenoids), phlorotannins	Benthic and floating thallus Long-term field experiments during austral winter (2015) and summer (2015/16).	Coquimbo (29° S–71° W), Concepción (36° S–72° W), Pta. Arenas (53–70° W), Chile	Tala et al. (2019)

Alginate

Durvillaea is an important resource for the alginate industry and has high alginate yields when compared to other brown seaweeds (Madgwick and Ralph 1972; Kelly and Brown 2000). Diverse studies have shown that alginate content in *Durvillaea* varies depending on the developmental stage (recruits, juveniles, and adults), the region of the thallus (holdfasts, stipes, and blades), and cell zones (peripheral, cortical, and medullary cells) (Moss and Naylor 1953; Madgwick and Ralph 1969, 1972; South 1979; Cheshire and Hallam 1985; Kelly and Brown 2000). Depending on the extraction methods, alginate yields (% of dry weight) can vary from 37 to 57% for *D. antarctica*, from 45 to 62% for *D. potatorum*, and from 51 to 66% for *D. willana*; with a M/G ratio of 4, 3.17, and 2.57, respectively (Panikkar and Brasch 1996). The difference in M/G ratio is related to morpho-functional responses, according to the highly hydrodynamic habitats, where it provides flexibility for blades and stipes, and more rigidity to the holdfast. Lower alginate yields were determined in former studies for *D. potatorum* and *D. willana* with ranges from 21 to 35% (see Table 2 in Madgwick and Ralph 1972).

Durvillaea potatorum sensu *lato* showed that blades and stipes contain alginates rich in mannuronic acid, whereas in the holdfast alginates are rich in guluronic acid. Moreover, a decrease in alginate yield was detected in blade tips—51.6%, and in the holdfast—35.8% (Cheshire and Hallam 1985). Similar variation in tissue content and composition were found for *D. antarctica* and *D. willana* with an alginate yield ranging from 30 to 55% (Kelly and Brown 2000). Apparently, this is a common pattern detected in *Durvillaea* species (Moss and Naylor 1954; Delepine et al. 1970; South 1979). The higher levels of alginate in blades have been related to their diffuse growth pattern with continuous production of new tissue as an important component within the entire blade. The cortex tissue in stipes showed high alginate levels compared with peripheral and medullar portions in *D. potatorum* (Madgwick and Ralph 1972; Kelly and Brown 2000).

Seasonal variations in environmental conditions can also change the content of alginate due to its effect on photosynthetic and growth. However, the greater variability observed within the thallus, between individuals, and over time produced no clear patterns. Kelly and Brown (2000) described a lack of a seasonal trend in alginate content or composition for *D. antarctica* and *D. willana*. However, a decrease in alginate from autumn to spring in blades and stipes of *D. potatorum* (Madgwick and Ralph 1972; Cheshire and Hallam 1985) and from summer to winter in blades of *D. antarctica* (Delépine et al. 1970), were previously described.

Nutritional composition

Nutritional and mineral composition of *Durvillaea* allows understanding the energy and organic materials available to the next trophic level, and its importance as human food. The nutritional composition usually includes quantification of moisture, ash, proteins, lipids, and carbohydrates (soluble and insoluble fiber). Some studies also include vitamins, minerals, and fatty acids profiles (Table 2). As the alginate contents, the nutritional composition can vary due to multiple abiotic and biotic factors. Blades and stipes of *D. antarctica* from the Kerguelen island showed similar nutritional composition whereas holdfast showed less ash and high dry matter and insoluble fiber (Lawrence 1986). The composition varies a little with respect to the thallus size. By contrast, Ortiz et al. (2006) described higher levels of ash (26%) and lipids (4%) in stipes compared to blades (18% and 0.8%, respectively) in the same species. Westermeier (1987) described seasonal and size variations in the nutritional composition of *D. antarctica* from southern Chile. The results showed that carbohydrates were higher in summer and the concentrations increased with size, whereas proteins had an irregular pattern. In general, holdfast and stipes from adult thallus showed a higher level of proteins (18–25%) with a maximum by mid and end of summer. Lipids in adult thallus varied between 2 and 8% with a fluctuating increase every 3 months.

Considering the importance of *D. antarctica* as food in Chile (referred to us as cochayuyo), Astorga-España et al. (2017) evaluated the change in nutritional composition of different dishes including cochayuyo bread, cochayuyo hamburgers, cochayuyo fettuccine. The study highlights the features of prepared food with levels of low lipid (4 to 8.5%), moderate protein (10 to 13%), and highly variable dietary fiber (4 to 19% dw). Moreover, fatty acid profiles showed a contribution of polyunsaturated fatty acids (PUFAs), such as linoleic acid and α-linolenic. Hot-air drying process applied to fresh samples of *D. antarctica* produced a decrease in crude fiber and total carbohydrate and an increase in ash, fat, and crude protein levels (Uribe et al. 2017).

Seaweeds are rich in a variety of minerals and metals. Nevertheless, information about *Durvillaea* species is limited (Table 2). Ash levels mostly represent the mineral content, and it can vary from 20 to 50% of dry weight, depending on the tissue zone (Madgwick and Ralph 1972; Lawrence 1986; Westermeier 1987; Ortiz et al. 2006). Mineral profiles in stipes of *D. potatorum* showed that potassium (5.1%), sodium (4.6%), magnesium (2.9%), and calcium (2%) were the major elements (Madgwick and Ralph 1972). Similar results were observed for *D. antarctica*, and Smith et al. (2010) also mentioned the high level of arsenic (27 mg kg^{-1} dry). However, this value is low on wet basis as it considers the New Zealand regulation that applies to seaweed as food.

There is little available information about fatty acid and amino acid profiles in *Durvillaea* species. Virtue and Nichols (1994) describe lipid classes, fatty acid, and sterol profiles for *D. potatorum* by comparing commerciality dried, fresh, and beached thallus. Lipid content and polyunsaturated fatty acids (PUFAs) levels decreased in dried and beached samples from 57% of PUFAs to 22%, respectively, which are products of oxidation of PUFAs. The 9% of the total lipids correspond to sterols in fresh *D. potatorum* (1.1 mg g^{-1} dry weight) and 99% is represented by fucosterol. This level decreases to 62% in the beached samples (Virtue and Nichols 1994). The most abundant fatty acid detected in stipe and blade of *D. antarctica* was C18:1ω9 (oleic acid) with 25% following by 10% of C18:2ω6 (linoleic acid). The eicosanoid precursor C20:4ω6 (arachidonic acid) was only detected in blades with 11% (Ortiz et al. 2006).

Only Ortiz et al. (2006) determined the amino acid profile in dried samples of *D. antarctica* from Chile detecting all essential amino acids except tryptophan. Stipes showed high levels of aspartic acid and histidine (> 1000 mg (100 g)$^{-1}$ of proteins) while in blades, glutamic acid and methionine were prevalent.

Other constituents

Phlorotannins, polymers of phlorogucinol units (1,3,5-trihydroxybenzene), are the most abundant phenolic compounds in brown seaweeds in soluble and insoluble forms inside the cells. Biochemical and physiological functions of phlorotannins have been associated with anti-herbivory and microbial defenses, as an effective antioxidant, in metal sequestration, and as photoprotector against UV-radiation (Swanson and Druehl 2002; Singh and Sidina 2013). Also, phlorotannins are important components of the cell wall and can be rapidly synthesized after thallus damage (Singh and Sidina 2013). The phlorotannins in *D. antarctica* have been included in studies related to the effect of environmental conditions on ecophysiological responses in lab and field experiments (Table 2). The concentrations can vary with season and latitude (Tala et al. 2013, 2016). Concentrations between 6 and 25 mg g^{-1} dw for soluble fraction and between 3 and 8 mg g^{-1} dw for insoluble have been detected in blades of *D. antarctica* (Cruces et al. 2012, 2013). The content of the soluble fraction can show a variation between 10 to 35 mg g^{-1} dw in spring and summer (Tala et al. 2013). High levels over 50 mg g^{-1} dw have been detected in *D. antarctica* from high latitudes (Tala et al. 2016).

Composition of tocols (tocopherols and tocotrienol) can vary with respect to the thallus portion in *D. antarctica* with a higher concentration in blades (~ 1113 mg kg^{-1} of lipids) compared with stipes (~ 267 mg kg^{-1} of lipids) (Ortiz et al. 2006). No information is available about the vitamin levels and compositions in *Durvillaea* species.

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