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ORIGINAL PAPER

Phenology, biomass and productivity of sub-Antarctic *Ruppia filifolia*

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Abstract Seagrasses play important ecological roles in shallow coastal ecosystems from tropical to sub-polar seas. *Ruppia filifolia* (Phil.) Skottsberg is the seagrass with the world's southernmost distribution but with virtually unknown biology and ecology. The goal of this study was to identify the ecological roles that *R. filifolia* might play in sub-Antarctic environments through the assessment of the development and primary productivity of this aquatic flowering plant. We monitored biomass and shoot density, rhizome growth and the presence of reproductive structures during 1 year in Skyring Sound, sub-Antarctic Chile. *Ruppia filifolia* forms perennial meadows with high biomass (124–293 g DW m^{-2}) and shoot density (1800–5300 shoot m^{-2}), a continuous presence of vertical stems and a rhizome plus root to shoot biomass ratio >1. Plant development shows a unimodal seasonal pattern with flowering in spring, and fruiting and maximum growth during summer. An average rhizome plastochrone of 37 days and median rhizome elongation of 27.5 cm $plant^{-1}$ $year^{-1}$ rank *R. filifolia* as a slow-growing seagrass. Primary productivity varied from 0.5 to 4.2 g DW m^{-2} day^{-1}, resulting in an annual primary production of 700 g DW m^{-2}. *Ruppia filifolia* in sub-Antarctic environments might play ecosystem roles (carbon sequestration, sediment stabilization, structural habitat, nutrition sources) as important as those played by seagrasses in tropical or temperate coastal environments.

Keywords Rhizome plastochrone · Vegetative development · Seagrass · Macrophyte

Introduction

Seagrasses are aquatic angiosperms that form key coastal ecosystems from tropical to sub-polar seas owing to their contribution to biological productivity, biodiversity maintenance, nursery habitat, nutrient cycling, carbon sequestration and export, sediment stability and shoreline protection, as well as being bioindicators of coastal environmental conditions (Spalding et al. 2003; Orth et al. 2006). Under current global changes, however, the worldwide distribution of seagrass meadows is rapidly declining (Orth et al. 2006; Waycott et al. 2009), yet these angiosperms remain understudied in some areas. Along the Pacific coast of southern South America, for instance, little to no information is available on the seagrass distribution, community structure, or ecological relationships. Besides seagrasses, other species of euryhaline aquatic flowering plants can form significant meadows in coastal aquatic environments—ranging from freshwater, to brackish, to hyperhaline and continental saline waters—and have wide

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distributions similar to those of the cosmopolitan genus *Ruppia* (den Hartog 1981). Knowledge of the biology and ecology of *Ruppia* species, in particular for *Ruppia maritima* L. and *Ruppia cirrhosa* (Petagna) Grande, is abundant and shows that their socio-ecological and economic role in shoreline ecosystems may be as important as those of seagrasses (Verhoeven 1980a, b; Ward et al. 1984; Kantrud 1991; Mannino and Sarà 2006).

Although debated (den Hartog and Kuo 2006), *Ruppia* species living in marine environments are regularly included in comprehensive seagrass treaties (Short and Coles 2001; Green and Short 2003). The name *R. filifolia* was proposed by Skottsberg (1916), and it has been used since then to refer to *Ruppia* plants living in freshwater and brackish coastal lagoons of southern Patagonia, Tierra del Fuego and the Falkland (or Malvinas) Islands, as well as the fjords and channels surrounding the Strait of Magellan (Moore 1973, 1983; Alvarez et al. 2010; Ito et al. 2010; San Martín et al. 2011; Mansilla et al. 2013). The names *Ruppia* sp. (Mazzella and Gambi 1993) and *R. maritima* (Dusén 1900; Short et al. 2007) have also been used to refer to *Ruppia* plants in the region. The abundant knowledge about the biology and ecology of some *Ruppia* species contrasts sharply with the very limited information available on *R. filifolia*, a taxon classified as “data deficient” by the International Union for the Conservation of Nature (IUCN 2014). *Ruppia filifolia* has been identified as the seagrass species with the world’s southernmost distribution (Short et al. 2007), and it is present in the sub-Antarctic tip of South America. The important ecological roles that other *Ruppia* species play in coastal aquatic systems throughout the world suggest that *R. filifolia* might also play key ecosystem functions in sub-Antarctic waters.

The goal of the present study was to identify the ecological roles that *R. filifolia* might play in southern South America by assessing the development and primary productivity of this species. Rhizome growth, biomass and shoot density of the meadow, and the presence of reproductive structures were monitored for 1 year. We compared the biomass of *R. filifolia* in sub-Antarctic Chilean waters to data reported for other *Ruppia* species in various regions around the world and also evaluated the reproductive phenology for consistency with former descriptions of the species.

Study area

Skyring Sound is a fjord with limited marine and tidal influence connected to the Strait of Magellan, sub-Antarctic Chile (Fig. 1a). The annual average air temperature is 6 °C, with a strong gradient of west-to-east rainfall (>6600 to <1000 mm year^{-1}) and dominant, strong winds from the west (annual average speed 3.7 m s^{-1}, average maximum speed 13.4–8.8 m s^{-1}; Schneider et al. 2003). The eastern shores of Skyring Sound harbor patchy meadows of *R. filifolia* to a depth of 4.5–5.3 m with biomass of 80 g dry weight (DW) m^{-2} (Mansilla et al. 2013), and it is the locality where the species was first described (Skottsberg 1916). Air temperature in this part of the fjord varies between 1.5 and 8.6 °C (average daily minima and maxima, respectively), the average daily solar radiation is 116 W m^{-2}, and the annual rainfall is 988 mm year^{-1} (Schneider et al. 2003). Dominant winds induce an eastward flow of surficial water with salinity of 18 (psu), temperature between 4.5 °C (winter) and 10.5 °C (summer), and dissolved oxygen concentration above 8 mg l^{-1} (Kilian et al. 2007). This study was performed at three sites near the mouth of the Pérez River, on the north coast of Skyring Sound (Fig. 1b). The main meadow for this study was site 1 (S1), with additional data collected in two other meadows, site 2 (S2) and site 3 (S3), located 800 m to the west and 1500 m to the east, respectively, of site 1 (Fig. 1c), all at 3 m water depth.

Methods

Biomass and density of shoots and vertical stems

Biomass and densities of shoots, vertical stems and rhizome apices of *R. filifolia* were estimated from three core samples (Duarte and Kirkman 2001) collected five times in S1 (November 2011, March, July and October 2012, and January 2013) and three times in S2 and S3 (November 2011, March and October 2012). All core samples were collected using a 20-cm-diameter stainless steel corer that was inserted to a depth of 40 cm in meadow sediment by SCUBA divers. The samples were washed to eliminate the sediment and detritus, placed in plastic bags and transported inside coolers to the laboratory for processing within the following 48 h. The number of shoots, vertical stems and rhizome apices of *R. filifolia* in each sample was counted to estimate their density (number m^{-2}) in the meadow. Biomass of *R. filifolia* was fractioned into leaves, vertical stems and rhizomes plus roots, then dried at 70 °C for 48 h to estimate their dry weight (DW). Dry weights in core samples were used to calculate meadow biomass and the relative allocation of biomass to plant parts using the rhizome plus root to shoot (leaves plus vertical stems) biomass ratio (RSR; Stevenson 1988).

Plastochrone of rhizome internodes and growth

The growth of *R. filifolia* was estimated by marking horizontal rhizomes in situ and retrieving them after

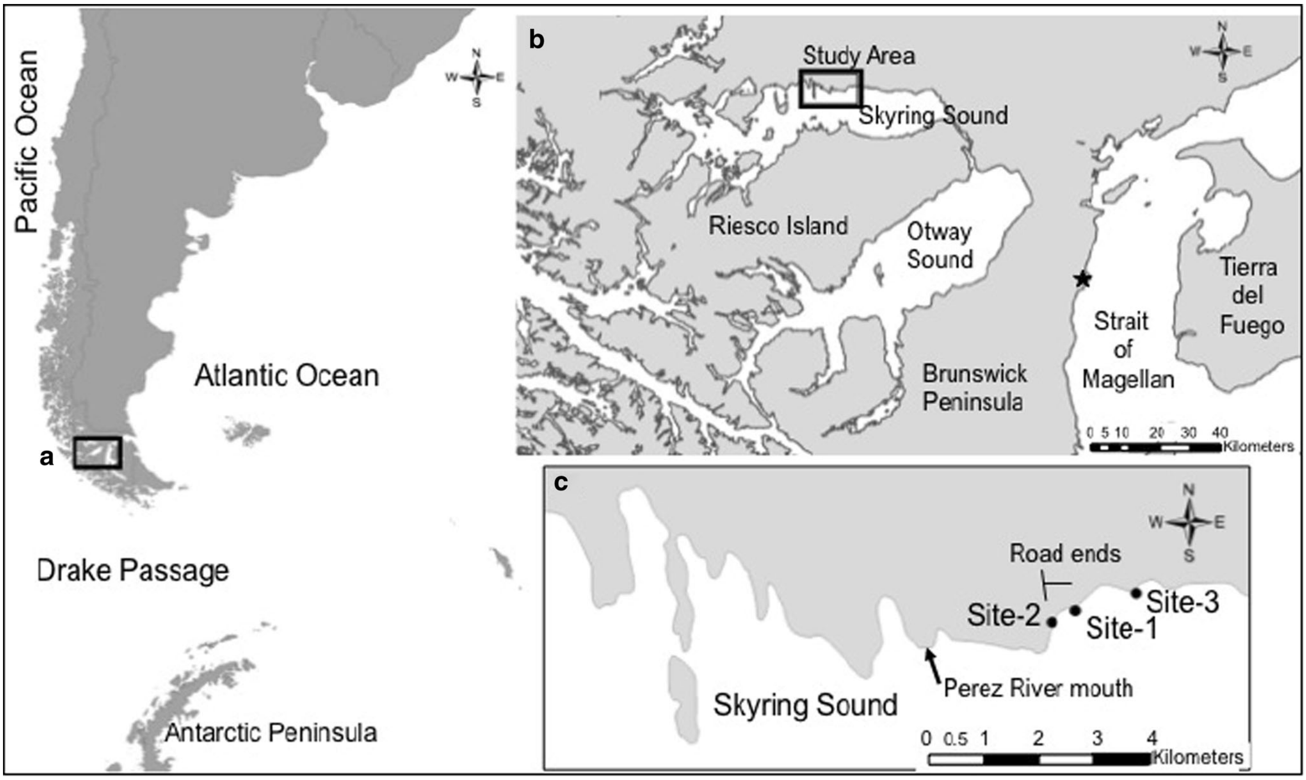

Fig. 1 Study sites in Skyring Sound, sub-Antarctic Chile, southern tip of South America. The star (*inset b.*) represents the city of Punta Arenas, a 2-h drive (150 km) to the study area in Skyring Sound. *Inset c.* shows the three study sites by the road's end and the mouth of the Pérez River: site 1 (S 52°32′46.80″, W 71°56′49.10″), site 2 (S 52°32′58.40″, W 71°57′27.10″) and site 3 (S 52°32′37.10″, W 71°55′31.00″), each 800 m west and 1500 m east of site 1, respectively

60–70 days. Marking was used to determine the plastochrone interval of a rhizome internode (P_R), that is, the number of days taken to produce a new internode by the rhizome (Short and Duarte 2001). The apices of horizontal rhizomes in the meadow were located by SCUBA divers, and a labeled cable tie was placed around the 3rd or 4th rhizome internode, counting from the apex. The number of internodes between the marked internode and the apex for each plant was recorded. No rhizomes had any branches between the marked internode and apex at the time of marking. Five marking periods were completed: 7–30 November 2011 (23 days), 8 December 2011–9 February 2012 (63 days), 9 February–18 April 2012 (69 days), 20 April–20 June 2012 (61 days) and 25 July–9 October 2012 (71 days). The number of rhizomes marked at the beginning of the marking period varied between 17 and 39, and the number of marked rhizomes that were retrieved at the end of the marking period varied between 16 and 31.

The number and length of all rhizome internodes and the number and length of branches between the marked internode and rhizome apex were counted and measured. The biomass (g DW after 48 h at 70 °C) of the leaves, rhizome and roots of each marked rhizome was recorded and divided by rhizome length (cm) to calculate the rhizome-specific leaf and rhizome plus root biomass (g DW cm^{-1} of rhizome). The P_R was calculated as the number of days between marking and retrieval divided by the number of new internodes produced by the apex. For each marked rhizome (i.e., one rhizome apex), the length of the internodes between the marked one and the apex was averaged (cm $internode^{-1}$) and divided by its P_R (days $internode^{-1}$) to estimate the elongation rate (cm $apex^{-1}$ day^{-1}). Adding the lengths of all the branches produced by a rhizome and dividing this by the number of days between marking and retrieval calculated the elongation rate of the branches. The total elongation rate of each marked rhizome was calculated as the sum of the elongation rates of the main rhizome and the branches (cm $apex^{-1}$ day^{-1}). The rhizome-specific leaf and rhizome plus roots biomass were multiplied by the total elongation rate of the rhizome to calculate the daily production rate (mg DW $apex^{-1}$ day^{-1}).

Reproductive phenology

A minimum of ten vertical stems were hand-collected by SCUBA divers in November 2011, March and April 2012, placed individually in plastic bags and transported to the laboratory to measure their length and obtain their dry weight. Vertical stems were considered reproductive when they developed flowers and fruits. The density of reproductive stems in S1 was estimated twice, once in March and once in April 2012. Twenty 50 × 50-cm quadrats were randomly placed throughout the meadow on each sampling date, and the number of vertical stems bearing reproductive structures (inflorescences), number of inflorescences in each reproductive stem and number of fruits in each inflorescence within each quadrat were counted by SCUBA divers. The length of the peduncle of the inflorescences was measured in a minimum of ten reproductive stems. The density of fruits in the meadow was calculated as the density of reproductive stems times the number of inflorescences per reproductive stem times the number of fruits per inflorescence.

Data analyses

ANOVA was used to evaluate the differences in biomass, density of shoots, vertical stems and rhizome apices, length and dry weight of vertical stems, and length of inflorescence's peduncle between sampling dates (random factor). Two-way ANOVA was used to evaluate differences of biomass between sites and sampling dates, both considered as random factors. The ANOVA assumption of variance homogeneity among groups was confirmed using Cochran's *C* test, and post hoc multiple comparisons of group means were performed using the Tukey's honestly significant difference (HSD) test.

A Kruskal-Wallis test and post hoc multiple comparisons of mean ranks of all pairs of groups were used to evaluate differences in P_{R}, average length of rhizome internodes between the marked internode and rhizome apex, the elongation rate of the rhizome's main axis and branches, and the daily total production (leaves, rhizome and roots) of the rhizomes between marking periods.

All statistical analyses were performed using STATISTICA 7.1 software (Statsoft Inc. 2005).

Results

Biomass and density of shoots and vertical stems

Shoot biomass (Fig. 2a) was lowest in November 2011, highest in March 2012 and decreased afterwards (ANOVA, $F_{4,9} = 7.45$, $p = 0.006$). The vertical stem biomass was highest in March 2012 and January 2013 and lowest in July 2012 ($F_{4,9} = 4.80$, $p = 0.024$). The rhizome and root biomass was highest in March 2012 and lowest in October 2012 and January 2013 ($F_{4,9} = 7.85$, $p = 0.005$). Total biomass (Fig. 2b) was higher in March 2012 than on other sampling dates ($F_{4,9} = 9.81$, $p = 0.002$). Except for July 2012, the RSR was higher in November 2011 than on the other sampling dates ($F_{4,9} = 9.41$, $p = 0.003$).

Shoot density (Fig. 2c) reached the maximum in March 2012 and the minimum in January 2013 ($F_{4,9} = 3.95$, $p = 0.040$). The density of vertical stems was highest in March 2012 and lowest in October 2012 ($F_{4,9} = 3.78$, $p = 0.045$). The density of rhizome apices showed a similar temporal pattern with an increase from November 2011 to March 2012 and a reduction afterwards (Fig. 2d), but the high variance of this variable in the last sampling dates rendered the ANOVA not significant ($F_{4,9} = 1.33$, $p = 0.330$).

Total biomass of *R. filifolia* was higher in S1 and S3 than in S2 (Fig. 3a site: $F_{2,4} = 12.19$, $p = 0.020$), and it was also higher in March 2012 than in November 2011 and October 2012 (date: $F_{2,4} = 25.65$, $p = 0.005$). The RSR was not different between sites ($F_{2,4} = 2.23$, $p = 0.222$) or sampling dates ($F_{2,4} = 1.38$, $p = 0.350$). Tukey's HSD test indicated that the significant interaction between site and sampling date ($F_{4,17} = 5.27$, $p = 0.006$) was driven by the value of RSR in S1 in November 2011, which was higher than any other value recorded (Fig. 3b).

Plastochrone of rhizome internodes and growth

The P_{R} increased ($H_{4,n=110} = 50.84$, $p < 0.001$) from a median of 11.5 days in November 2011 to 21 days in December 2011–February 2012, 17.5 days in February–April 2012, 30.5 days in April–June 2012 and 71 days in July–October 2012 (Fig. 4a). The average length of rhizome internodes between the marked internode and the rhizome apex was higher ($H_{4,n=116} = 51.37$, $p < 0.001$) in November 2011 and December 2011–February 2012 than in the other marking periods (Fig. 4b). The elongation rate of the rhizome decreased ($H_{4,n=116} = 53.85$, $p < 0.001$) from a median value of 0.15 cm apex^{-1} day^{-1} in November 2011 to 0.09, 0.08, 0.03 and 0.02 cm apex^{-1} day^{-1}, respectively, in the following marking periods (Fig. 4c).

The percentage of marked rhizomes that branched ranged from 46 (November 2011) to 93 % (December 2011–February 2012). The elongation rate of rhizome branches increased ($H_{4,n=70} = 23.78$, $p < 0.001$) from a median of 0.03 cm apex^{-1} day^{-1} (November 2011) to 0.06 cm apex^{-1} day^{-1} (December 2011–February 2012), decreasing to 0.02, 0.01 and 0.01 cm apex^{-1} day^{-1} in subsequent marking periods (Fig. 4d).

The median daily total production rate (leaves, rhizome and roots) of the marked plants was around 2 mg DW apex^{-1} day^{-1} in November 2011 and December 2011–February 2012 (Figs. 5, 6) and decreased ($H_{4,n=116} = 40.79$, $p < 0.001$) to 1.3, 0.6 and 0.4 mg DW apex^{-1} day^{-1} in February–April 2012, April–June 2012 and July–October 2012, respectively. The multiplication of the median daily production rate of a rhizome apex by the duration of the marking period in days and by the density of rhizome apices (estimated from core samples)

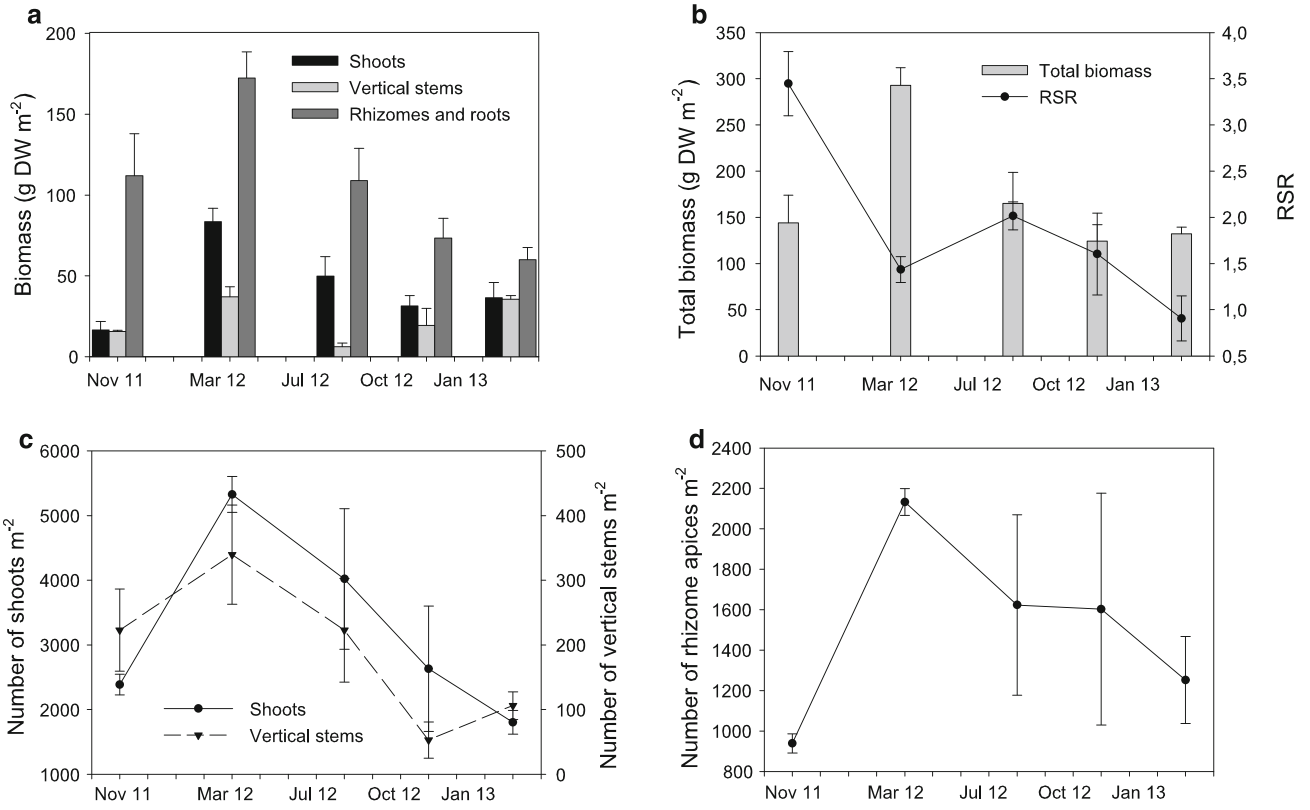

Fig. 2 **a** Biomass of shoots, vertical stems and rhizomes and roots; **b** total biomass and rhizomes plus roots to shoots (RSR) biomass ratio; density of (**c**) shoots and vertical stems and **d** apices of rhizomes of *R. filifolia* in site 1, near the mouth of Pérez River, Skyring Sound (Chile). *Error bars* indicate +1 SE (*bar plots*) or ±1 SE (*line plots*)

as well as the summation of all marking periods gives an estimate of an annual productivity of 630 g DW m^{-2} year^{-1} for the rhizome apices of *R. filifolia*. The productivity associated with vertical stems should be added to this amount. Unlike horizontal rhizomes, the vertical stems do not grow continuously, but decay and detach from the meadow. Hence, the maximum biomass of vertical stems in the meadow may be considered an estimate of the annual productivity of this plant part. A first estimate is the maximum biomass of vertical stems recorded (37 g DW m^{-2} in March 2012). A second estimate is 112 g DW m^{-2}, which resulted from multiplying the maximum density of vertical stems (340 stems m^{-2} in March 2012) by the maximum average weight of a single vertical stem (0.33 g DW stem^{-1} in April 2012). The average of these two estimates, 74 g DW m^{-2}, was chosen as an estimate of the annual productivity of vertical stems in the meadow, leading to a *R. filifolia* meadow productivity of 700 g DW m^{-2} year^{-1}.

Reproductive phenology

Flowers started to develop in vertical stems in spring (November 2011), and fruits were observed in summer (February and March 2012 and January 2013) and autumn (April 2012). The length of the vertical stems increased from 19.6 ± 3.9 cm per stem in November 2011 to 24.9 ± 2.0 cm in March 2012 and 31.8 ± 2.4 cm in April 2012 ($F_{2,41} = 3.53$, $p = 0.038$). Biomass of the vertical stems increased from 0.14 ± 0.03 g DW per stem (November 2011) to 0.23 ± 0.3 g DW (March 2012) and 0.33 ± 0.3 g DW in April 2012 ($F_{2,41} = 9.58, p = 0.0003$). No differences in length ($F_{1,17} = 0.10$, $p = 0.755$) or biomass ($F_{1,17} = 1.40$, $p = 0.252$) were detected between reproductive vertical stems bearing inflorescences with fruits and non-reproductive vertical stems in March 2012. The density of reproductive stems was 46.5 ± 3.6 stems m^{-2} in March 2012 and 44.2 ± 5.3 stems m^{-2} in April 2012, and represented 13.7 % of the density of vertical stems in the meadow (considering shoot density data from March 2012). The length and biomass of reproductive vertical stems were not different between March and April 2012 ($F_{1,18} = 2.65$, $p = 0.121$; $F_{1,18} = 2.08, p = 0.166$; respectively).

Reproductive stems (87 % in March 2012 and 89 % in April 2012) have up to four inflorescences with an average number of inflorescences per reproductive stem of 1.2 ± 0.1 in March 2012 and 1.1 ± 0.02 in April 2012. The number of fruits per inflorescence varied between 1

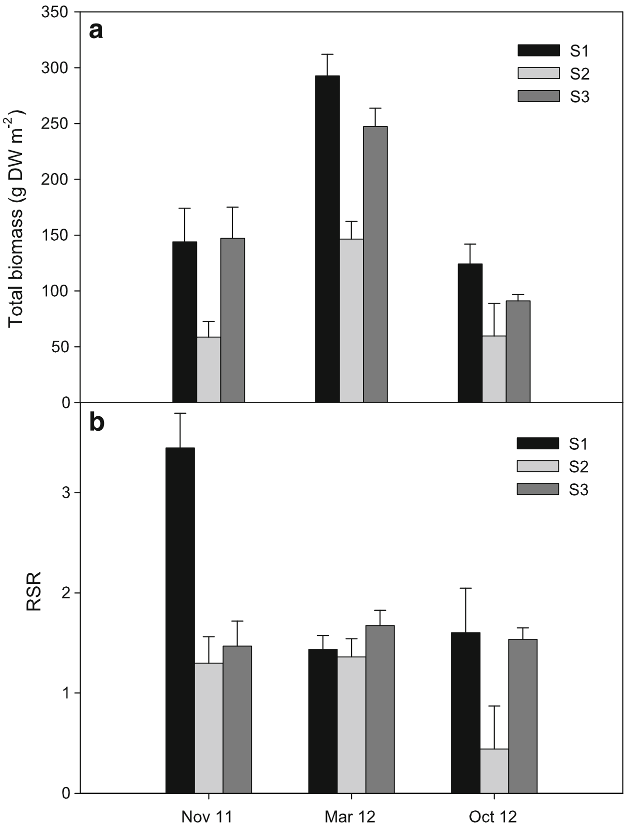

Fig. 3 Total biomass and rhizome and root to shoot (RSR) biomass ratio of *R. filifolia* in three sites (S1, S2 and S3) near the mouth of the Pérez River in Skyring Sound (sub-Antarctic Chile). *Error bars* indicate +1 SE

and 7 with averages of 2.4 ± 0.2 in March 2012 and 1.8 ± 0.1 in April 2012. The length of the inflorescence's peduncle was similar ($F_{1,51} = 0.76$, $p = 0.388$) in March 2012 (5.9 ± 0.2 cm) and April 2012 (5.6 ± 0.3 cm). The density of fruits was 134 ± 33 fruits m^{-2} in March 2012 and 87 ± 20 fruits m^{-2} in April 2012.

Discussion

We present the first in-depth assessment of the reproductive phenology, vegetative development and primary productivity of *R. filifolia*, a poorly known species (IUCN 2014) and the seagrass with the world's southernmost distribution (Short et al. 2007). This seagrass forms perennial meadows that maintains a remarkable biomass (124–293 g DW m^{-2}) in sub-Antarctic environmental conditions throughout the year. The development of *R. filifolia* in Skyring Sound shows a unimodal seasonal pattern with maximum values during summer. Our compilation of data on the total biomass and RSR of *Ruppia* species at the annual maximum (Online Resource 1) shows that *R. filifolia, R. cirrhosa* and *R. megacarpa* achieve a higher biomass than *R. maritima* and *R. polycarpa* ($H_{4,n=128} = 10.48$, $p = 0.033$; Fig. 6a) and that *R. filifolia* maintains a higher RSR than any other species ($H_{4,n=51} = 12.63$, $p = 0.013$; Fig. 6b). The high RSR suggests that *R. filifolia* might have a higher potential for carbon burial in the sediment than other *Ruppia* species. Indeed, we observed the presence of a rhizome mat (i.e., a 5–10-cm-thick, compacted layer of rhizomes, roots and sediment) of this species in several meadows at Skyring Sound during a previous survey (Mansilla et al. 2013) and erosional morphologies (scarps, blowouts; Patriquin 1975; Clarke and Kirkman 1989) in the edges of some meadows. Also such meadow features suggest that *R. filifolia* might play an important role in sediment stabilization in Skyring Sound.

The meadows of *R. filifolia* in our study sites are characterized by a high density of shoots (1800–5300 shoots m^{-2}), especially during summer, and vertical stems are continually present in the meadow (even in winter) with a seasonal pattern similar to that of shoots. High shoot densities are common in meadows of other *Ruppia* species, with maximum values of 2300–3647 shoots m^{-2} for *R. megacarpa* (Carruthers et al. 1999), 3705–16,400 shoots m^{-2} for *R. cirrhosa* (Mannino and Sarà 2006; Pergent et al. 2006) and 8630–48,000 shoots m^{-2} for *R. maritima* (Dunton 1990; Moore 2004; Cho and Poirrier 2005).

The growth of *R. filifolia* in Skyring Sound shows a clear seasonality with short P_R and high rhizome elongation rates from spring to summer (November–February) and long P_R and low elongation rates from autumn through winter (April–October). Rhizome branching was highest throughout the summer, from December to April. The average P_R of *R. filifolia* (37 days) is longer than that reported for fast-growing seagrasses (4–15 days for *Halophila* spp., *Syringodium* spp., *Halodule* spp., *Thalassia* spp., *Thalassodendron* spp., *Zostera* spp.) and shorter than that of slow-growing seagrasses (48–125 days for *Amphibolis* spp. and *Posidonia* spp.; Short and Duarte 2001). Thus, *R. filifolia* ought to be ranked as a medium- to slow-growing seagrass, though its rhizome growth may be high (P_R of 11 days) during the austral summer. *R. cirrhosa*, in contrast, is a faster growing species, with a P_R of 3–6 days during the active growth period (Verhoeven 1979). Similar to P_R-based comparisons, the median elongation rate of the rhizome in *R. filifolia* (27.5 cm plant^{-1} year^{-1}, branches included) ranks this species as a slow grower within seagrasses that show horizontal rhizome elongation rates from 2 to 356 cm apex^{-1} year^{-1} (Marbà and Duarte 1998).

The unimodal pattern of growth in *Ruppia* species, with high values during spring/summer and maximum meadow biomass achieved in summer/autumn, is the norm in temperate climates (Verhoeven 1979; Obrador and Pretus

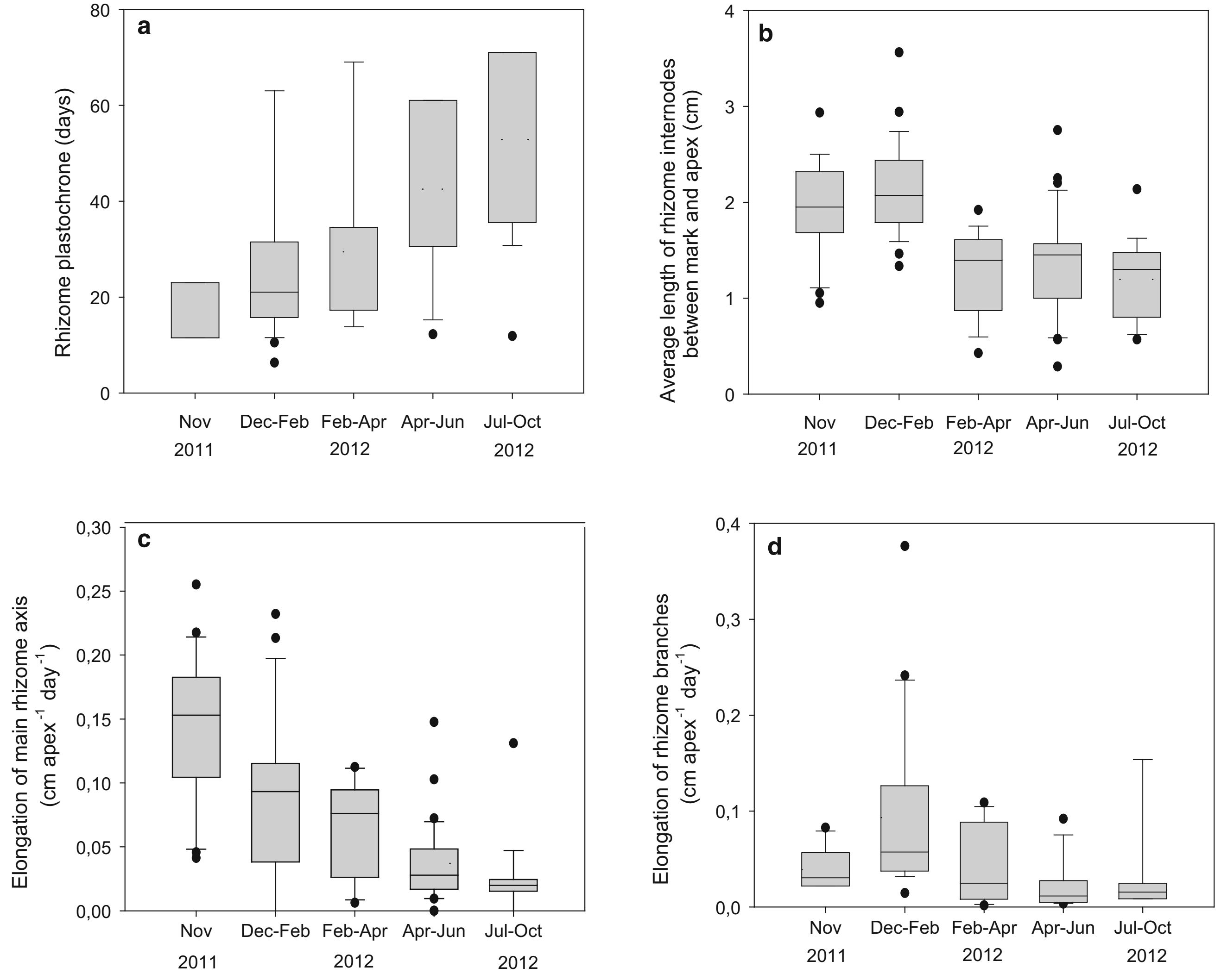

Fig. 4 Growth of *R. filifolia* in site 1, near the mouth of the Pérez River, Skyring Sound (sub-Antarctic Chile): **a** rhizome plastochrone, **b** the average length of rhizome internodes between the marked internode and the rhizome apex, and daily elongation rates of the (**c**) main rhizome and (**d**) rhizome branches. *Lower* and *upper* ends of *boxes* represent 25th and 75th percentiles of data distribution. The continuous and *dotted lines* inside *boxes* represent the median and mean of data. The *lower* and *upper whisker caps* represent the 10th and 90th percentiles, and the *circles* represent data points beyond them

2010), although two biomass peaks are possible in subtropical climates (Dunton 1990; Cho and Poirrier 2005). *R. filifolia* frames its vegetative development between water temperatures of 4 and 10 °C, rendering it a "cold water" plant compared to other *Ruppia* spp. (Verhoeven 1979). Also the flowering and fruiting of *Ruppia* spp. is usually unimodal and follows the biomass cycle (Verhoeven 1979; Harrison 1982). Flowers of *R. filifolia* were observed in December and January in the Falkland Islands (Moore 1983) and from November to February in Skyring Sound (Mazzella and Gambi 1993; this study) where fruits were observed from January to April and germinating seeds and seedlings in November, suggesting that *R. filifolia* is able to reproduce sexually at water temperatures below 10 °C. The investment in sexual reproduction of *R. filifolia* in Skyring Sound is lower than that of other *Ruppia* spp. that produce thousands of seeds per square meter (Volleberg and Congdon 1986; Cho and Poirrier 2005; Vromans et al. 2013) because the majority of vegetative shoots may become reproductive (Harrison 1982).

Ruppia filifolia at our site 1 showed very high productivity rates during summer (4.2 g DW m^{-2} day^{-1}) that decreased an order of magnitude during winter (0.5 g DW m^{-2} day^{-1}). The maximum productivity rates place *R. filifolia* in the middle range of values reported for seagrasses (0.1–25 g DW m^{-2} day^{-1}, Duarte and Chiscano 1999). For example, annual production of *R. maritima* and *R. cirrhosa* meadows in European waters ranged between

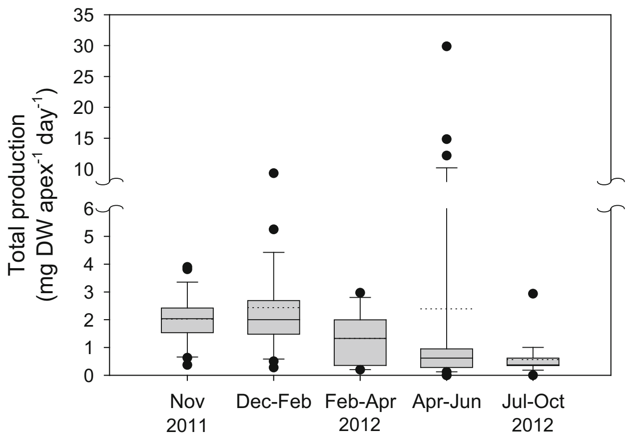

Fig. 5 Daily production rate of leaves, rhizome and roots by a rhizome apex of *R. filifolia* in site 1 near the mouth of the Pérez River in Skyring Sound, sub-Antarctic Chile. *Box plot* as in Fig. 4

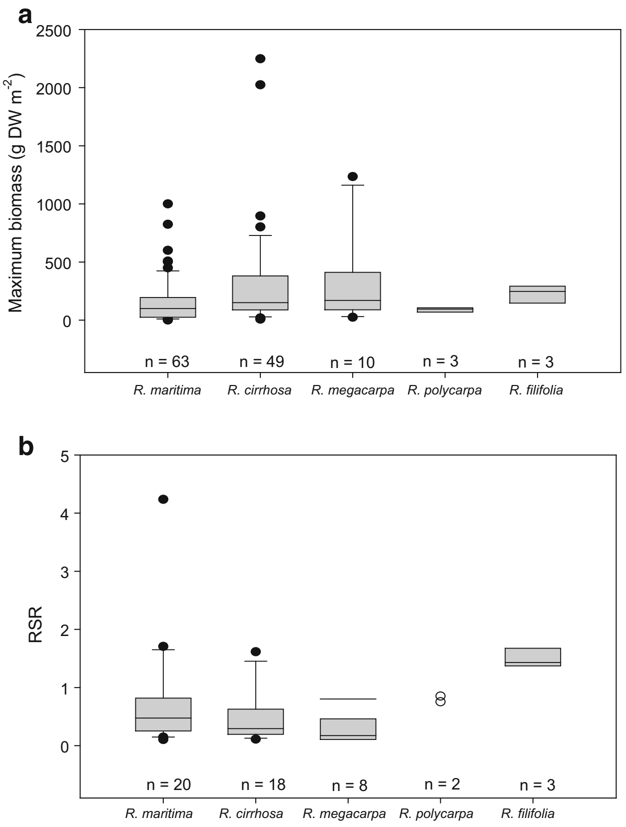

Fig. 6 Comparison of biomass and RSR at the annual maximum achieved by *R. filifolia* in Skyring Sound, sub-Antarctic Chile (this study) and other *Ruppia* spp. (data obtained from the literature; Online Resource 1)

53 and 400 g DW m^{-2} and up to 919 g DW m^{-2} (Verhoeven 1980a; Calado and Duarte 2000; Obrador and Pretus 2010). An annual production of 75–500 g DW m^{-2} was estimated for *Ruppia* sp. in Western Australia (Congdom and McComb 1979). The average daily (1.7 g DW m^{-2} day^{-1}) and annual production (700 g DW m^{-2}) of *R. filifolia* implies that this species might also play an important trophic role in the shallow ecosystem of Skyring Sound. *Ruppia* meadows there provide habitat and food to several organisms (Kantrud 1991). Black-necked swans (*Cygnus melancoryphus*) and small fishes (*Patagonotothen tessellata*) were regularly observed feeding on *R. filifolia* during this and parallel studies in the region (e.g., Hüne and Vega 2015). The structural habitat and nutrition sources provided by meadows of *R. filifolia* in Skyring Sound are thereby important to associated fauna, considering that these meadows maintain significant biomass and shoot density throughout the year.

In conclusion, *R. filifolia*, the seagrass with the world's southernmost distribution, and possibly the only sub-Antarctic seagrass, forms perennial meadows important to maintaining sediment stability, structure and biomass year round, as well as contributing a primary productivity comparable to that of other *Ruppia* species and other seagrasses worldwide. Furthermore, *R. filifolia* may play other key ecosystem functions, such as carbon sequestration, structural and nursery habitats, and nutritional resources, in the subpolar environment of Skyring Sound at the southern tip of South America.

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Conflict of interest We present no conflicts of interest to describe.

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